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THE INHERITANCE OF THE FLOWER COLOUR AND THE SEED COLOUR IN LUPINUS ANGUSTIFOLIUS

BY *CARL HALLQVIST*
WEIBULLSHOLM, LANDSKRONA

SEVERAL types of flower colour and seed colour are known in *Lupinus angustifolius* since long ago. The data have been brought together in »Die Züchtung der landwirtschaftlichen Kulturpflanzen», where FRUWIRTH (1919) mentions the occurrence of blue, light blue, rose (probably identical with my bluish red) and white flower colours. It is also stated here that dark seed colour and coloured flowers are correlated, as well as white seed colour and white flowers. FRUWIRTH hybridized blue and white types and found that blue flower colour and dark coloured, marbled seeds were dominant over white flower colour and white seeds. In F_2 the hybrids segregated in the ratio 3 : 1.

According to HARZ (in Landwirtschaftliche Samenkunde) there is also found a variety named *leucospermum* with coloured flowers and white seeds. The existence of this variety has been doubted by KAJANUS. According to him, the cause of proposing this variety must be due to the occurrence of white seeds in samples of blue flowered varieties. The fact that white flowers become coloured at a later stage (see pag. 302) may also account for the fact, especially since the intensity of this colour varies greatly in response to varying environmental conditions. No type with white seeds combined with coloured flowers in earlier stages has been found in my material.

The most complete investigation hitherto made of the inheritance of the flower colour in *Lupinus angustifolius* has been published by VESTERGAARD (1919). He also finds that the blue and white colours segregate in the ratio 3 : 1. He also crossed red and white types and succeeded in obtaining a synthesis of the blue colour in F_1 and F_2, which segregated regularly in 9 blue, 3 red and 4 white. The red type in VESTERGAARD's cultures is probably also identical with my bluish red.

The seed colour has been investigated by FRUWIRTH (1915) and KAJANUS (1912). FRUWIRTH has obtained a type with dark, self-coloured seeds. He has studied its inheritance, and he has arrived at very peculiar results. I have had no type of this kind in my material.

KAJANUS has classified different types of seed colour, but no study of their inheritance has been made by him. I am much indebted to KAJANUS for receiving material of the different types of seed and flower colours.

THE MATERIAL.

The following pure bred lines have been used as starting material.

1. *Flower colour*: Blue — *Seed colour*: Earth-brown, marbled and white punctured. The ordinary seed colour.
2. » : » — » : White punctured and earth-brown, not marbled. This is the variety »Weibull's Meteor».
3. » : Tinged blue — » : Earth-brown, marbled and white punctured.
4. » : Bluish red — » : Earth-brown, marbled and white punctured.
5. » : Violet — » : Rust-brown, marbled and white punctured.
6. » : White — » : White.

In the course of the experiments the following new types have been obtained as recombination products:

1. *Flower colour*: Violet — *Seed colour*: Rust-brown and white punctured, not marbled.
2. » : Pure red — » : Rust-brown, marbled and white punctured.
3. » : Tinged red — » : Earth-brown, marbled and white punctured.

The colour of the flower changes with age in this lupine as well as in other species of the genus. The different types are, however, very distinct, and no difficulty is met with in classifying the types. While in all coloured types coloration appears in the vegetative organs, as in the cotyledons, in the petioles, in the bracts and sepals, no such coloration is found in the white flowered types, where the enumerated parts are pure green.

DETAILS OF THE TYPES.

THE FLOWER COLOUR.

The blue type (Pl. II, fig. 1). Standard blue, wings blue with the upper edge of the upper third bluish violet and with a bluish white lower part, strongly marked with deep blue coloured nerves. Also the lower edge of the lower part lighter. Keel white with blue nerves and with an intensive dark blue beak. The two upper sepals of the calyx quite blue, the two lateral, smaller ones also almost blue coloured, the median, strongly developed sepal green with the exception of blue coloured tip and nerves. . The membraneous bract with blue spots and striae concentrated in the margin of the leaf. This makes the unopened inflorescence quite blue. The colour of the axis of the inflorescence in the upper part strongly blue, disappearing downwards. The colour of the flower more intensive with age.

The tinged blue type (Pl. II, fig. 5). Standard of flowers just opening almost white on the inside with only a faint tinge of blue; the outside, the tip and the flanks with a weak but distinct blue colour. The median and basal parts white. The upper edge of the wings white, the lower edge with a faint blue colour, disappearing from the place of union downwards. Keel white with no trace of colour (the beak of the keel of the blue type deep blue coloured). The yellow anthers visible through the keel.

The blue coloured parts become larger with age, and the coloration becomes more intensive. At last a violet tinge appears on the inside of the standard and on the upper and outer parts of the wings. However, the colour of the oldest flowers of this type is not anything like the colour of the youngest flowers of the blue type. The keel remains uncoloured. The colour of the bracts and sepals as in the blue type, the colour of the unopened inflorescence, consequently, blue. The colour of the axis of the inflorescence also blue.

The violet type (Pl. II, fig. 2). Standard violet with blue nerves,

with a bluish tinge at the base. Wings violet with blue nerves, the lower edge from the place of union downwards with a bluish tinge; the upper edge lighter, in its upper part, above the place of union, reddish violet. Keel white with violet nerves and blackish violet beak. Blue coloured parts enlarging with age, the colour intensifying. Sepals and bracts violet, the distribution of colour as in the former type. The colour of the axis brownish.

The bluish red type (Pl. II, fig. 3). Standard red with blue nerves. Wings red with blue nerves, the colour weaker in the back parts of the upper edge, and in the basal parts on the whole. The area above the union of the wings either quite blue or sharply defined by a blue line. Keel white with blackish red beak. Older flowers with a diffuse blue colour, intensifying with age. Sepals and bracts reddish with a tinge of blue. The distribution of the colour in these organs as in the blue type. The axis bluish red.

Bluish red is ordinary called red in *Lupinus angustifolius*. Bluish red is probably the colour called rose by FRUWIRTH and red by VESTERGAARD, as mentioned in the above.

The pure red type (Pl. II, fig. 4). I have intentionally adopted this name to mark it off from the bluish red type with which it is easily confused. As regards the red colour no difference is seen in the both types, but every trace of blue colour in the flower and in other parts is absent from the pure red. The axis is brownish red. The difference between the two colour types is quite distinct and errors in classifying them are out of question to the trained observer; a less trained eye, however, may have some difficulty in separating the types. This difference is also noticeable in the seed colour. Cp. the description of the seed colour, pag. 304, and the characteristic of the seed colour in immature stages, pag. 331.

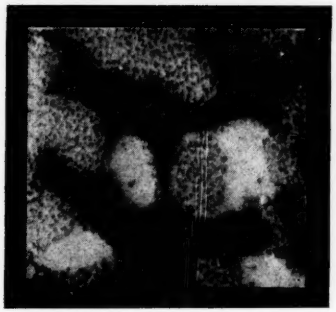
The tinged red type (Pl. II, fig 6). Standard and wings with a faint, yellowish tinge of rose. Keel as in the tinged blue type, without colour, even in the beak. Sepals, bracts and axis as in the bluish red type.

The white type. Standard and wings in early stages pure white, coloured with age. Intensity of the colour varies with different environmental conditions; it is sometimes so marked that a flower in the proper stage of development hardly deserve to be called white coloured. An old individual of a white line seems to be stronger coloured than the »dilution forms» tinged blue and, particularly, tinged red, since the colour of these is diffuse, while the colour of the whites is concentrated in the wings.

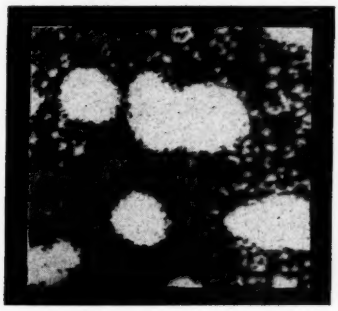
There is one important point of difference, however, between the flowers of the whites and those of the tinged types, viz. the coloration of the latter ones even in early stages. The young flowers of the whites show no trace of colour; the sepals, bracts and axis are quite green.

THE SEED COLOUR.

The seed colour of *Lupinus angustifolius* depends on the presence of pigment in the palisades of the seed coat, according to the investigations of KAJANUS and FRUWIRTH. The figure reproduced in the work of FRUWIRTH (1915, pag. 218) shows that the pigment layer is defined to the centre of the palisade cells. The ordinary colour of the



a ($^{12}/_{1}$)
Marbled; white flecks, dark areas composed of closely packed pigment grains, the lighter areas with scattered grains.



b ($^{12}/_{1}$)
Non-marbled; white flecks, dark areas as in *a*, the lighter areas lacking.

Fig. 1.

seed is this (Pl. II, fig. 8). On a lighter or darker coloured pearl-gray ground there is found an earth-brown marbling of varying limits together with white flecks sharply defined. When examined under a magnifying lens the characteristics of this coloration will be found (see fig. 1). The pigment grains are collected in small groups; the heaping up of these groups or the scattered occurrence of the groups give rise to the above mentioned characteristic colour schemes as shown in the figure. They are very closely heaped up in the dark marbled areas, they are more scattered in the pearl-gray fields, and in the white parts only sporadic dots are found. The limits between the different coloured areas are remarkably sharp. I have characterized this type as the earth-brown, marbled. KAJANUS mentions three

varieties of this type differing in the intensity and in the distribution of the colour; only the darker one of his types, which at the same time is the one generally found, has been used in my experiments, but seeds resembling the lighter, thin coloured types have often been found as modifications.

The fourth type proposed by KAJANUS has been used in one of my experiments (Pl. II, fig. 7). It lacks the pearl-gray ground-colour; in its place the earth-brown marbling colour covers the whole surface of the seed with the exception of the white flecks. The pigment groups are found here only in two grades of density, sporadically in the white flecks and closely compacted in the earth-brown areas. The intermediate grades of density do not occur, and the gray colour, consequently, does not occur either (fig. 1 b). I have characterized this type as the earth-brown, not marbled. It is very easy to distinguish this type from the marbled as no transitions are found.

The earth-brown seed colour is found correlated with blue, tinged blue, bluish red and tinged red flowers, but is not found in violet, pure red and white.

The rust-brown seed colour, (Pl. II, fig. 9 and 10) due to another kind of pigment, is not mentioned in the literature. This type includes also marbled and non-marbled varieties. The marbled variety (Pl. II, fig. 10) has a gray field, almost cream-coloured, a rust-brown marbling and white flecks. Seeds from the earth-brown type are sometimes modificatory rust-brown when poorly developed. If only sound and fully developed seeds are taken for comparison, no difficulty is met with in classifying the types. The rust-brown seed colour is found correlated with violet and pure red flowers.

The non-marbled variety of the rust-brown type has been obtained as a recombination product from my experiments. It also lacks the gray ground colour as does its earth-brown analogue. It may appear peculiar that the gray ground colour and the marbling colour of the three-coloured type depend on different quantities of the same pigment. The investigations of FRUWIRTH and KAJANUS as well as my own experiments bear out this fact, however, and it is further strengthened by the observations made on the colour of seeds still immature and enclosed in the green pods. The gray as well as the marbled parts of the seed have the same colour at this stage, and the difference is wholly one of intensity. In the earth-brown type there are two different grades of intensity of blue, in the rust-brown type of violet.

The white seed (Pl. II, fig. 11) has a faint rust-brown, hook-for-

med scar at the hilum; the whole surface of the seed is generally found to have a touch of the same marbling colour. Cp. the coloration of the white flowers when old.

I have only found white seeds in lines with white flowers.

As to the methods employed it should be stated that isolation by means of parchment bags has been used in all cases (with the exception of Nos. 228—236—20). Consequently, the families are all progenies from isolated mother plants. It seems, however, as were self-fertilization the exclusive method of fertilization in *L. angustifolius*. The families just mentioned (94 plants in all) showed no case of vicinism when allowed to seed whithout bagging, and the same has been found in other families with recessive flower colours not mentioned in the tables, viz. 3 tinged blue, 2 tinged red and 1 pure red families, 105 individuals in all.

No case of vicinism has been found in these 199 cases in spite of the most favourable opportunities of hybridization. Further investigations on this point are in progress. The same has been pointed out by VESTERGAARD, who did not use any isolation in his experiments.

The following crosses have been made between the types discussed in the above.

TABLE OF CROSSES.

Cross 1:	White flower colour » seed colour	×	Blue flower colour Earth-brown, marbled seeds
» 2:	Violet flower colour Rust-brown, marbled seeds	×	Blue flower colour Earth-brown, non-marbled seeds
» 3:	Bluish red flower colour Earth-brown, marbled seeds	×	Blue flower colour Seed colour as female parent
» 4:	Tinged blue flower colour Earth-brown, marbled seeds	×	Blue flower colour Seed colour as female parent
» 5:	White flower colour » seed colour	×	Tinged blue flower colour Earth-brown, marbled seeds
» 6:	Violet flower colour Rust-br. marbled seed colour	×	White flower colour » seed colour

Cross 7:	Bluish red flower colour Earth-brown, marbled seeds	×	White flower colour » seed colour
» 8:	Tinged blue flower colour Earth-brown, marbled seeds	×	Violet flower colour Rust-brown, marbled seeds
» 9:	Bluish red flower colour Earth-brown, marbled seeds	×	Violet flower colour Rust-brown, marbled seeds
» 10:	Bluish red flower colour Earth-brown, marbled seeds	×	Tinged blue flower colour Seed colour as female parent

GENETICAL FORMULAE.

Before discussing the segregations it seems desirable to give a summary of the genetical formulae. The formulae shall be fully discussed later.

R: a factor for pure red flower colour and rust-brown seed colour; it is, in addition, the fundamental colour factor; the *rr*-types have white flowers and white seeds.

B: a bluing factor giving bluish red flowers and earth-brown seeds with *R*.

V: transforms the pure red colour into violet, necessitating the presence of *R; V* does not influence the seed colour.

The factors *B* and *V* give the full blue colour when both present; in the absence of *R* no coloration is attained by any of them. Thus the formula *RBV* is required for blue colour.

F: a factor necessary for the complete development of the colour. The colour produced by the other factors become diluted when *F* is absent. Blue becomes tinged blue, bluish red becomes tinged red. The diluted forms of violet and pure red have not yet been found. The seed colour is not influenced by this factor.

M: the marbling factor. The pigment in the seed coat becomes closely compacted in some parts and thinner in other when *M* is present. In the absence of *M* no marbling occurs the pigment being distributed evenly on the surface, interrupted only by white flecks.

The different constant phenotypes apart from the marbling are thus constituted as follows:

Blue	flower colour,	earth-brown	seed colour	= *RRBBVVFF*
Tinged blue	»	»	»	= *RRBBVVff*
Bluish red	»	»	»	= *RRBBvvFF*
Tinged red	»	»	»	= *RRBBvvff*
Violet	»	rust-brown	»	= *RRbbVVFF*
(?	»	»?	»	= *RRbbVVff*) not yet obtained.
Pure red	»	»	»	= *RRbbvvFF*
(?	»	»?	»	= *RRbbvvff*) not yet obtained.
White	»	white	»	= *rrBBVVFF*
»	»	»	»	= *rrbbVVFF* etc.

THE RESULTS OF THE SEGREGATIONS.

The detailed results of the segregations and the numerical relations within the different families are tabulated in tables 7—26, pp. 345—362. The numbers of individuals of the different families are rather small, as seen, and therefore it is not possible to decide upon the question whether within the families belonging to the same type of segregation small but significant differences are present, as for instance in the degree of linkage etc.; only the totals of the families with the same mode of segregation have been considered here. When treating the proportions between the F_3-families of different types of segregation only the relation between the constant dominants and the heterozygous families have been determined; the constant recessives have not been considered. Thus the proportions expected have been referred to the number 3 $(1 + 2)$ instead of 4 $(1 + 2 + 1)$ in the case of simple segregation. In the case of di-hybrid segregations the proportions have not been calculated from the constant 16, but each family from double dominant and simple recessive mother plants have been calculated from the numbers $1 + 2 + 2 + 4$ and $1 + 2$ respectively. It should also be mentioned that F_3-families with less than 20 individuals have not been considered.

It is to be expected, according to the genetical formulae, that all crosses between blue colour on the one side and tinged blue, bluish red, violet and the whites constituted *rrBBVVFF* on the other should give simple segregation, as each of these latter ones differ genotypically from the blue ones only by the absence of one factor. The same type of segregation should result, and for the same reason, when the earth-

brown seed of the blue flowers are crossed with the rust-brown in the violet and with the white seed of the whites. All these combinations have been made (crosses 1, 2, 3, 4), and both the F_2- and the F_3-generations have given the results expected.

Cross 1 (table 7).

White flower colour, » seed colour *rrBBVVFF* × blue flower colour, earth-brown seed colour *RRBBVVFF*

F_1 is blue and earth-brown, and the segregation in

F_2: 289 blue : 73 white, expected 271,5 : 90,5.

The difference = 17,5 is 2,1 times the standard error (8,24) and, consequently, somewhat great, yet it is not so large as to lie beyond the limits prescribed. F_3 was spoiled. The inheritance of the seed colour was not followed in this cross.

Cross 2 (tables 8—9).

Violet flower colour, rust-brown seed colour (*RRbbVVFF*) × blue flower colour, earth-brown seed colour (*RRBBVVFF*).

F_1 is blue with earth-brown seeds, and F_2 has given:

	215 blue :	73 violet	(table 8)
expected:	216	72	D/M = 1,0/7,35 = 0,14.

3 violet F_2-plants have given constant violet progenies in F_3 (table 9) with 247 individuals in all. Among 9 F_3-families from blue parent plants 1 has given a constant blue progeny (22 individuals), and 8 have segregated in:

	456 blue :	154 violet	
expected:	457,5	: 152,5	D/M = 1,5/10,69 = 0,14.

The results of the segregation in F_2 as well as in F_3 are, as seen, pretty satisfactory, although the proportions between the constant and the segregating F_3-families might have been better. Instead of the expected 3 : 6 proportions 1 : 8 was obtained. The low number of plants makes the deviation allowable. The seed colour was determined in F_2 in 209 blue and 69 violets; all blue were found to have earth-brown seeds, all the violets rust-brown seeds.

Cross 3 (tables 10—11).

Bluish red × blue flower colour, no difference in seed colour.
RRBBvvFF *RRBBVVFF*

F_1 is blue, and F_2 segregates in

122 blue : 40 bluish red (table 10)
expected: 121,5 : 40,5 D/M = 0,5/5,51 = 0,09.

The following segregation numbers were obtained in F_3:

296 blue : 101 bluish red
expected: 297,75 : 99,25 D/M = 1,75/8,63 = 0,20.

The relation between the number of constant and segregating families is 6 : 8, expected: 4,67 : 9,33. The constant blue families have 296 individuals in all. From 6 bluish red parent plants 202 individuals of the same colour were obtained. Thus the results are pretty well in accordance with the theoretical expectation.

Cross 4 (tables 12—13).

Tinged blue × blue flower colour, no difference in seed colour.
RRBBVVff *RRBBVVFF*

F_1, having the formula *RRBBVVFf* and heterozygotic in factor *F* only, is blue, but upon closer study it is found that a weakening of the colour has taken place. The influence of the *F*-factor is thus seen to be somewhat stronger in the duplex stage than in the simplex stage. The segregation numbers in F_2 as well as in F_3 are very good:

F_2 396 blue : 138 tinged blue (table 12)
expected: 400,5 : 133,5 D/M = 4,5/10,0 = 0,45
F_3 324 blue : 107 tinged blue (table 13)
expected: 323,25 : 107,75 D/M = 0,75/8,99 = 0,08.

The relation between the constant and the segregating F_3-families, 6 : 11, comes in addition as close as possible to the theoretical expectation, and the progenies of all tinged blue coloured plants investigated have been found to be constant in accordance with the theory.

Simple Mendelian segregation is to be expected in some other combinations according to the theory. No primary crosses have been made in these cases, but the F_3 of some di-hybrid crosses includes families from parent plants with the same kind of heterozygosis as that of the primary crosses if made. The proportions to be expected, 3 : 1, are found in all cases. The following cases should be observed:

Tinged blue × tinged red in F_3 of cross 10 (table 26),
Bluish red × pure red in F_3 of cross 9 (tables 23—24),
Violet × pure red in F_3 of cross 9 (table 24),
Bluish red × tinged red in F_3 of cross 10 (table 26).

Bluish red × white (*rrBBvvFF*) in F_3 of cross 7 (table 19),
Tinged blue × white (*rrBBVVff*) in F_3 of cross 5 (table 15),
Violet × white (*rrbbVVFF*) in F_3 of cross 6 (table 17).

With the exception of the combinations tinged red × white, with the constitution *rrBBvvff*, and pure red × white, with the constitution *rrbbvvFF*, all those combinations have been investigated, where simple segregation is to be expected, and the segregation has in all these cases followed normal and good proportions without any selection or other disturbances.

Three crosses have been made between whites on the one side and coloured but not blue types on the other. All theses combinations gave a synthesis of blue and segregated in F_2 in the ratios 9 : 3 : 4. The proportions found in F_3 substantiate the results and correspond with the hypothesis as well. These are the crosses 5, 6 and 7.

Cross 5 (tables 14—15).

White seed- and flower colours (*rrBBVVFF*) × tinged blue flower colour (*RRBBVVff*); earth-brown, marbled seed.
F_1 has slightly diluted blue flower colour and earth-brown seeds. The simplex stage of the factor *F* accounts for the slight dilution of the colour (Cp. cross 4).

F_2 53 blue : 10 tinged blue : 18 white (table 14)
expected: $45{,}_{56}$: $15{,}_{19}$: $20{,}_{25}$

$$\text{D/M}\ \frac{7{,}_{44}}{4{,}_{66}} = 1{,}_{60} \qquad \frac{5{,}_{19}}{3{,}_{51}} = 1{,}_{45} \qquad \frac{2{,}_{25}}{3{,}_{90}} = 0{,}_{58}$$

F_3 of the same cross gave:

337 blue : 127 tinged blue : 138 white (table 15)
expected: $338{,}_{62}$: $112{,}_{88}$: $150{,}_{5}$

$$\text{D/M}\ \frac{1{,}_{62}}{12{,}_{17}} = 0{,}_{13} \qquad \frac{14{,}_{02}}{9{,}_{58}} = 1{,}_{47} \qquad \frac{12{,}_{5}}{10{,}_{62}} = 1{,}_{18}$$

It is clear that the segregation of this cross takes place in the ratio 9 : 3 : 4, even if the deviations often lie beyond the limits of the standard error in each generation. When the results in F_2 and F_3 are summed up, however, the differences become smothed out, and the results conform to the theory, the quotients D/M being $0{,}_{45}$; $0{,}_{88}$; and $1{,}_{17}$ respectively. Also the rest of the results in F_3 corresponds with the hypothesis. The observed numerical relations are pretty well in accordance with the calculated as seen in the following.

158 blue : 48 tinged blue

expected: 154,5 : 51,5 $D/M = \frac{3,5}{6,22} = 0,56$

224 blue : 78 white

expected: 226,5 : 75,5 $D/M = \frac{2,5}{7,53} = 0,33$

179 tinged blue : 56 white

expected: 176,25 : 58,75 $D/M = \frac{2,75}{6,64} = 0,41$

The constant and the segregating families occur in a number, which is very near to the theoretical expectation. From 32 blue parent plants the result was:

7 constant blue : 13 9:3:4-segregates : 6 blue and tinged blue : 6 blue and white families

expected: 3,56 14,22 7,11 7,11

D/M $\frac{3,44}{1,78} = 1,93$ $\frac{1,22}{2,82} = 0,43$ $\frac{1,11}{1,94} = 0,58$

10 tinged blue F_2-plants gave in F_3:

5 constant tinged blue : 5 tinged blue and white families

expected: 3,33 : 6,67 $D/M = \frac{1,67}{1,57} = 1,06$

As seen the mode of segregation in this cross is typical of a synthetic cross. It should be noticed, however, that the synthesis does not originate through the coming together of a fundamental colour factor and the blue colour factors. This combination is realized already in the tinged blue parent plant. It is the meeting of the fundamental factor with the intensity factor *F* that makes the synthesis.

45 blue, 8 tinged blue and 5 white F_2-plants have been examined as to seed colour; all the blue and the tinged blue had earth-brown seeds, and all the whites had white seeds.

Cross 6 (tables 16—17).

Violet flower colour, earth-brown seeds × white flowers and seeds.

RRbbVVFF *rrBBVVFF*

F_1 had blue flowers and earth-brown seeds. In F_2 we expect, according to the theory, the ratios 9 : 3 : 4. We find:

27 blue : 16 violet : 8 white (table 16)

expected: 28,09 9,56 12,75

D/M $\frac{1,69}{3,54} = 0,48$ $\frac{6,44}{2,79} = 2,31$ $\frac{4,75}{3,09} = 1,53$

The number of individuals in the whites and in the violets seems to indicate quite other ratios than 9 : 3 : 4. The results obtained in F_3 show, however, that this ratio must be correct, and that the abnormal number in F_2 is a case of an unusual great deviation, although within the range allowed by the theory. From blue parent plants partly di-hybrids have been obtained showing the following numerical relation:

216 blue : 76 violet : 92 white (table 17)

expected: 216 72 96

D/M 0 $\frac{4}{7,65} = 0,52$ $\frac{4}{8,49} = 0,47$

partly mono-hybrids with the following numerical relations:

135 blue : 50 violet

expected: 138,75 46,25 D/M $\frac{3,75}{5,90} = 0,64$

169 blue : 43 white

expected: 159 53 D/M $\frac{10,0}{6,30} = 1,59.$

No constant blue families have been found, however. This is probably due to the small number of families. 13 families from blue mother plants, distributed in the following classes have been followed:

0 constant blue : 5 9:3:4-segregates : 4 blue and violet : 4 blue and white

expected: 1,44 5,74 2,89 2,89

3 constant violets and 5 3:1-segregating families have been obtained from violet plants. The proportion expected is 2,67 : 5,33 and the total number of individuals in the segregating families was:

242 violet : 93 white

expected: 251,25 : 83,75 D/M $\frac{9,25}{7,98} = 1,17$

One white plant gave a constant white progeny.

The seed colour in the F_2-plants has been examined in 26 blue plants, 14 violets and 6 whites. The colour of the seeds in the blue

plants was earth-brown, in the violets rust-brown and in the whites white.

Cross 7 (tables 18—19).

Bluish red flower colour, earth-brown seeds (*RRBBvvFF*) × white flowers and seeds (*rrBBVVFF*).

F_1 gave blue flowers and earth-brown seeds

F_2 41 blue : 15 bluish red : 17 white (table 18)

expected: 41,06 13,69 18,25

D/M $\frac{0,06}{4,24} = 0,01$ $\frac{1,31}{3,34} = 0,39$ $\frac{1,25}{3,70} = 0,34$

The numerical relations are good also in the F_3-generation:

F_3 100 blue : 30 bluish red : 42 white (table 19)

expected: 96,75 32,25 43

D/M $\frac{3,25}{6,51} = 0,50$ $\frac{2,25}{5,12} = 0,44$ $\frac{1,00}{5,68} = 0,18$

The mono-hybrid F_3-numbers are satisfactory even if not quite as good as the above; they are:

33 blue : 14 bluish red

expected: 35,25 11,75 D/M $= \frac{2,25}{3} = 0,75$

47 blue : 24 white

expected: 53,25 17,75 D/M $= \frac{6,25}{3,65} = 1,71$

33 bluish red : 7 white

expected: 30 10 D/M $= \frac{3}{3,22} = 0,93$

Blue coloured F_2-plants have given the following F_3-families:

2 constant blue : 5 9:3:4-segregates : 2 blue and bluish red : 2 blue and white

expected: 1,22 4,88 2,44 2,44

5 bluish red F_2-plants gave 4 constant bluish red and one 3:1-segregating family. The numbers to be expected are 1,66 constant and 3,34 segregating families. The class distribution in F_3 shows, as seen, very poor correspondence with the expectation; the inversion of the values would give almost the ideal relations. The possibility of such an inversion is not improbable when the small numbers of families are considered. 7 white flowering plants gave as many constant white families.

As to the seed colour the above mentioned whites and their progeny had all white seeds, the rest of the F_2-plants examined with regard to seed colour, 25 in all, had earth-brown seeds. 20 of these were blue coloured, the other 5 tinged blue.

The di-hybrid crosses just discussed, where *one* of the parents has been white follow the hypothesis exactly, and the results of the segregations are quite satisfactory. The group of di-hybrid crosses where both parents have been coloured, although not blue coloured, has now to be discussed (crosses 8, 9 and 10).

Cross 8 (tables 20—21).

Tinged blue flowers, earth-brown seeds (*RRBBVVff*) × violet flowers, rust-brown seeds (*RRbbVVFF*).

F_1 sligthly diluted blue, earth-brown seeds.

F_2 should segregate in blue, violet, tinged blue and tinged violet in the ratios 9:3:3:1, according to the hypothesis. The result was:

470 blue : 241 violet : 255 tinged blue (table 20).

Thus the expected mode of segregation has not been realized. A double recessive of the violet tinged type is lacking; mere chance is excluded on account of the great number of individuals. About 60 plants of this type are to be expected; however, since none has been obtained, a deviation 8 times the standard error has to be assumed, a deviation so large as to lie far beyond the allowed range. It could be argued, perhaps, that the absence of the *F*-factor did not influence the violet colour. This seems very improbable, as the number of the blue and tinged blue groups is abnormal, the former is too small, the latter too large to account for the ratios 9 blue : 3 tinged blue : 4 violet to be expected in such a case; the results obtained in F_3 also invalidate this argumentation. If valid, mono-hybrid families together with di-hybrids should be obtained from blue coloured F_2-plants, and mono-hybrid families in addition to the constant families should originate from tinged blue parent plants. This is not the case, however. The numerical relations showing the best correspondence with the numbers found are 2 blue : 1 violet : 1 tinged blue giving when applied to the number of individuals in question:

483 blue : 241,5 violet : 241,5 tinged blue

D/M $\frac{13}{15{,}5} = 0{,}84$ $\frac{0{,}5}{13{,}5} = 0{,}04$ $\frac{13{,}5}{13{,}5} = 1{,}0$

F_3 repeats this di-hybrid segregation with:

	1160 blue :	586 violet :	605 tinged blue
expect:	$1175{,}_{50}$	$587{,}_{75}$	$587{,}_{75}$
D/M	$\frac{15{,}_{50}}{24{,}_{2}} = 0{,}_{64}$	$\frac{1{,}_{75}}{21} = 0{,}_{08}$	$\frac{17{,}_{25}}{21} = 0{,}_{77}$

There are additional deviations from normal segregation to note. Constant blue flowered families, as well as 3:1-segregating families from blue parent plants, are wholly absent. All families from such parent plants give the di-hybrid type of segregation in the ratios 1 : 2 : 1. All families from violet and tinged blue parent plants are, furthermore, constant and do not show any segregation. All these deviations in the proportions of the families and of the phenotypes are characteristic of an absolute or close linkage.

It is dilution and the violet colour which, phenotypically seen, never or rarely enter into combination. Genotypically it is explained by assuming a repulsion between the factors *B* and *F*; the phenotypical correlation between violet and fully developed colour should, in other words, depend on the closeness between the factors representing bluish red and full colour according to the chromosome-theory. This depends of course on the construction of the factorial scheme. The violet colour caused by the factor *V* appears only when the *B*-factor has been excluded, and vice versa. Consequently, this inverse proportionality between the phenotypical manifestation and the genotypical mode of characterization will be found in all the following crosses, where linkage occurs. This would have been avoided had the CASTLE-MORGAN method of factor denotation been adopted (cp. MORGAN 1915, pag. 253). The genetical formulae would have been constructed in the following way: Blue = wild type; bluish red is caused by mutation of the *B*-factor, denoted *b*; we denote further violet colour by *v* instead of *bV*, and pure red by *bv* und not by *bvR*; tinged colour is caused by the absence of *F* (= *f*) as before. The repulsion in cross 8 would then be caused by the close linkage between the factors *f* and *v*. The fact that our case corresponds in colours and in the mode of segregation with analyses previously made favoured, however, the adoption of the traditional factor denotation.

The degree of linkage can not be determined, as no recessives appear. It may be absolute, but partial linkage of a relatively high degree is also conceivable. The results obtained allow but an approximate estimate of the minimal value of its strength. The total number of individuals of the di-hybrid segregation in F_2 and F_3 is 3317.

Assuming a relative frequency between recombinated gametes and non-recombinated ones (the former category not yet found in this case) of 1 : 10 : 10 : 1 (*BF* : *Bf* : *bF* : *bf*) a number of 6,85 double recessives would originate, and the probability of their non-appearance is about 1 : 1000. Thus it is very improbable that the non-recombinated gametes are less than 10 times the recombinated ones. They are rather much more numerous. This belief is strengthened when the numerical relations of the F_3-families are considered.

The F_3-method for determining gametic ratios will be further treated in the following, where a case of partial linkage is discussed (pag. 323). As it is shown here the gametic ratio may be determined by the proportions between F_3-families of two different groups belonging to different types of segregation.

A number of 60 segregating families of repulsion type, 22 constant violets and 44 constant tinged blue have been obtained in the present cross. They all belong to *one* of the family-groups just mentioned, the other group, where the families segregating in the ratios 3 : 1 form the bulk, is altogether absent. As in the »F_2-analysis» the minimal value of the strength of the linkage may thus be determined and it is found that the F_3-method gives much better result. The minimum ratio 1 : 10 just calculated is, according to the F_3-analysis, out of question; the ratio 1 : 36 may be assumed with just the same probability to be the minimum. The gametic representation would necessitate 7 families out of the 126 grown belonging to the absent group, and the probability that all these are excluded is about 1 : 1000. It is therefore rather safe to assume a higher frequency of the non-recombinated gametes. The probability of the exclusion of the said families is about 1 : 25 at a gametic frequency of 1 : 100; the probability of their exclusion and their presence are equal first at a gametic frequency of 1 : 300, when the total number of families is 126. These calculations show clearly the advantage of using the F_3-method in cases of repulsion. It has been found to give much greater precision than the analysis of the F_2, even when the number of the families has been relatively small. It is clear that the present case is a case of close linkage, and it is of great interest to continue the cross.

The result of the examination of the seed colour in this cross gave: 40 violets with rust-brown seeds, 87 blue and 59 tinged blue with earth-brown seeds.

Cross 9 (tables 22—24).

Bluish red flowers, earth-brown seeds (*RRBBvvFF*) × Violet flowers, rust-brown seeds (*RRbbVVFF*).

F_1 Blue flowers, earth-brown seeds.

The deviations from expectation in F_2 are great also in this cross. All the expected phenotypes are present, it is true, and pure red is obtained for the first time, but the ratio 9 : 3 : 3 : 1 is greatly deformed. It is clear that the deviation is due to disturbances in the gametic representation in the shape of repulsion. It should be mentioned that

TABLE 1.

Reference number	Generation	Frequency of phenotypes					Ass. coeff. of observed phenotypic ratio	Standard error M	Ass. coeff. of calcul. phenotypic ratio	Gametic ratio	Crossover percentage
		BV	*bV*	*Bv*	*bv*	Total					
		1	2	3	4	5	6	7	8	9	10
						Repulsion.					
1	F_2	556	269	226	15	1066	0.7587	± 0.0587	0.7567	1 : 3.1 : 3.1 : 1	24.4
2	F_3	1142	540	542	20	2244	0.8290	± 0.0153	0.8305	1 : 3.9 : 3.9 : 1	20.4
3	F_4	9	8	3	0	20	—	—	—	—	—
4	$F_2+F_3+F_4$	1707	817	771	35	3330	0.8248	± 0.0285	0.8233	**1 : 3.8 : 3.8 : 1**	**20.8**
						Coupling.					
5	F_3	241	28	30	62	361	0.8935	± 0.0301	0.8935	4.7 : 1 : 1 : 4.7	17.6
6	F_4	204	28	32	33	297	0.7651	± 0.0663	0.7656	3 : 1 : 1 : 3	25.0
7	F_3+F_4	445	56	62	95	658	0.8182	± 0.0303	0.8510	**3.9 : 1 : 1 : 3.9**	**20.4**

there is a remarkably great number of recessives in the family 597—18 (table 22), and the segregation agrees with the proportions 9 : 3 : 3 : 1. The number of individuals, however, is not large enough to substantiate the view that the type of segregation differs from the type characteristic of the rest of the families, and this is not either to be expected. Unfortunately no seed could be obtained from this family, and therefore no F_3-generation could be raised.

From the result of the segregation it is seen at once that the gametic frequency is about 1 : 3 or 1 : 4. In order to arrive at an accurate determination of the ratio the method of COLLINS and BRIDGES (COLLINS 1912, BRIDGES 1914) was adopted. The association coefficient (YULE's ass.) of the segregating ratios obtained has thus been calcula-

ted (col. 6, table 1) and compared with a series of ass. coefficients of several ideal phenotypical ratios belonging to various gametic ratios. The results are put together in table 1 (pag. 317).

The accuracy of the values obtained in this or similar ways, as EMERSON (1916) has pointed out, depends greatly on the question whether or not the proportions between certain groups of the zygotic distribution series meet the demands which have to be raised (apart from the characteristic distribution at the gametic frequency in question). The characteristic feature of di-hybrid segregation values with 9 : 3 : 3 : 1 as ground-type, whether free combination or linkage of the coupling or repulsion type are exhibited, is the equality of the middle groups ($Bv = bV$, or $\frac{Bv + bV}{2}$). The first group, BV, must be three times the last one when the sum of the middle groups ($Bv + bV$) is subtracted from the first group. That is, $BV - (Bv + bV) = 3\ bv$, or $\frac{BV - (Bv + bV)}{3} = bv$. These points are demonstrated in the scheme, pag. 320. If different linkage values are obtained for the same characters the accuracy of the different values should be controlled from this point of view. Such a control of the values in this cross shows that in two cases remarkable deviations from expectation have resulted, viz. in the case of number 1 of the F_2, table 1, and in ref. number 6 in F_4 in coupling. In the first case the difference between the middle groups is rather great. It is seen, however, that this deviation is of no importance as the value of the association coefficient, calculated with the middle groups reduced to half of the sum of values actually obtained, changes in so small a degree that it still shows the best correspondence with the gametic ratio 1 : 3,1. Thus the deviation from other calculations showed by this ratio does not depend on the difference in the values of the middle groups.

In the second example, viz. the coupling in F_4 (ref. number 6), the last group, bv, is found to be too small in relation to $BV - (Bv + bV)$. The values obtained are 33 and 144 respectively. The ideal ratio would be 44,25 : 132,75, consequently a deficit of more than 11 recessives. If the association coefficient is calculated on the ideal ratio just mentioned the gametic frequency becomes 3,3 : 1 instead of 3 : 1, and the linkage value becomes 23,3 instead of 25. It is therefore to be concluded from the mere disproportion between the first and the last groups that the result with regard to the coupling in F_4 (ref. number 6) is doubtful.

TABLE 2.

Ass. coeff. of the phenotypic ratios corresponding to various gametic ratios.

Gametic ratio	Coupling	Repulsion
1,5 : 1	0,3494	0,3425
2,0 : 1	0,5575	0,5422
2,5 : 1	0,6845	0,6646
3,0 : 1	0,7656	0,7445
3,5 : 1	0,8198	0,7986
4,0 : 1	0,8575	0,8373
4,5 : 1	0,8847	0,8659
5,0 : 1	0,9049	0,8875
5,5 : 1	0,9114	0,9043

The linkage values obtained may be further tested with the help of the standard error of the ass. coeff. determined according to YULE (1900) and listed in table 1, col. 7, and with the help of the table of the association coefficients for a series of gametic ratios (table 2). Both coupling and repulsion values answering to about 3 : 1 and 1 : 3 respectively are obtained if the threefold standard error is subtracted from the association coefficient of the observed values. This value marks the lower limit, and it is very improbable that the numerical values correspond to a gametic ratio lower than this. The corresponding upper limit lies higher. The ass. coeff. of repulsion reaches a value differing from the ass. coeff. by three times the standard error first at the gametic ratio 1 : 5,5, and the limit lies still higher in question of coupling values. When the simple standard error is used, the corresponding limits are 1 : 3,5 and 1 : 4,3.

Thus it is seen that the standard errors allow great fluctuations of the linkage values, and the reliance of these may be questioned. It is very significant, however, that the gametic ratios of the coupling and the repulsion values show such a close correspondence, in the former case $n = 3{,}9$, in the latter $n = 3{,}8$. It is very improbable, indeed, that the two different cases should give extreme deviations from a common middle value in the same direction in both cases. The allowed range of fluctuation diminishes greatly in such cases, and the linkage values obtained from the numerical relations of the different phenotypes, therefore, must be considered more reliable than is indicated in the above control.

The gametic ratio may be determined in still another way. Technical difficulties in raising a sufficient number of individuals in the back crosses render this method impossible in the case of *Lupinus angustifolius*. The gametic ratio may be calculated directly from the proportions between the families of certain segregating types in F_3, and the result of the F_2-analysis may be checked with the help of these proportion values. The linkage values have been determined in certain cases in this way by MULLER (1916) in *Drosophila*.

	AB	*Ab*	*aB*	*ab*
	1	*n*	*n*	1
AB	1	*n*	*n*	1
Ab	*n*	n^2	n^2	*n*
aB	*n*	n^2	n^2	*n*
ab	1	*n*	*n*	1

a

	AB	*Ab*	*aB*	*ab*
	n	1	1	*n*
AB	n^2	*n*	*n*	n^2
Ab	*n*	1	1	*n*
aB	*n*	1	1	*n*
ab	n^2	*n*	*n*	n^2

b

Fig. 2.

By the usual checker scheme it is easy to demonstrate that in cases of repulsion (fig. 2 a) the relation between the number of families in the centre and in the middle parts of the periphery is a simple and constant function of the gametic ratio. The repulsion segregates and the constant simplex recessives belong to the centre — their number is $4n^2$ — the families of different types segregating in 3 : 1, 8n in number, belong to the middle parts of the periphery. Thus the relation between these two groups is $\frac{4n^2}{8n} = \frac{n}{2}$. The corner-families of the periphery do not need to be considered, partly because of the easy task to recognize them in the F_3-analysis and to exclude them from the calculations, partly because of the small number of these families which makes possible their neglecting especially in cases of close linkage, that is when n attains large values.

The same results are arrived at in cases of coupling with regard to families occupying other places in the quadrate (fig. 2 b). Here it is the families in the centre which may be omitted. The corner-families give the numerator $4n^2$, while the denominator, 8n, is still the characteristic value of the middle parts of the periphery. Thus in cases of

coupling the corners and the middle parts of the periphery are compared, and the relation between these groups is $\frac{n}{2}$ as said before. Other combinations, naturally, may be made within the F_3-families in order to determine the relative gametic ratio, but this is the most suitable partly because of its simplicity, partly because of he fact that only the largest groups are used, which insure the most reliable results. Furthermore, the method makes use of families resulting from coupling as well as from repulsion at the same time. A summary of the

TABLE 3.

List of the number of families of different segregating types in F_3 and F_4 from cross 9.

Type of segreg. in parent fam.	Colour of parent plant	Kinds of phenotypes in the families	Types of repulsion ratios	$4n^2$	$8n$	other groups
Repulsion	Blue	Blue	Constant	—	—	1
	»	Blue + violet + bl. red + pure red	Coupling	—	—	6
	»	» » » »	Repulsion	43	—	—
	»	Blue + violet	3 : 1	—	18	—
	»	» + bluish red	3 : 1	—	19	—
	Violet	Violet	Constant	28	—	—
	»	Violet + pure red	3 : 1	—	18	—
	Bluish red	Bluish red	Constant	32	—	—
	»	Bluish red + pure red	3 : 1	—	13	—
	Pure red	Pure red	Constant	—	—	2
		Total		103	68	9
Coupling	Blue	Blue	Constant	6	—	—
	»	Blue + violet + bl. red + pure red	Coupling	9	—	—
	»	» » » »	Repulsion	—	—	1
	»	Blue + violet	3 : 1	—	4	—
	»	Blue + bluish red	3 : 1	—	2	—
	Violet	Violet	Constant	—	—	1
	»	Violet + pure red	3 : 1	—	1	—
	Bluish red	Bluish red	Constant	—	—	4
	»	Bluish red + pure red	3 : 1	—	1	—
	Pure red	Pure red	Constant	5 [1]	—	—
		Total		20	8	8
		General total		123	77	—

[1] Fictitious value $= \frac{\text{constant} + \text{coupling}}{3} = \frac{6+9}{3}$ (see text)

families belonging to different segregating types (F_3 and F_4) of cross 9 is given in table 3. Column 1 tabulates the families, which in the case of repulsion on the part of the parent families occupy the centre of the quadrate, and those which in cases of coupling occupy the corners. Thus all the families forming the denominator are tabulated in this column. Column 2 tabulates the families segregating in the ratio 3 : 1, that is the numerator. For sake of completeness the rest of the families is put together in col. 3, which is not used, however, when the linkage values are calculated. The total of the first col. is 123 families, the second is 76, and the result is the following equation:

$$\frac{n}{2} = \frac{123}{76};\ n = 3{,}2$$

The standard error of the proportions 123 : 76 is $\pm$ 4,85. This figure, simple or taken three times, added or subtracted, gives rise to displacements in the proportions of the families and corresponding changes in the gametic ratios as seen in the following:

1M	127,85 : 71,15	corresponding to	n = 3,6
	118,15 : 80,55	» »	n = 2,9
3M	137,55 : 61,45	» »	n = 4,5
	108,45 : 90,55	» »	n = 2,4

It should be stated that with regard to the constant pure red families showing coupling a fictitious value of their number has been used for the following reason. As the number of the pure red plants had been determined already in F_2, and as it further appeared certain that all should show constancy in F_3, no need of raising F_3-families from them was present. In order to be able to use the formula, however, a value representing one third of the number of the corner-families left has been used, in this case 5, which stands in about the same relation to the sum of the rest of the families as the pure reds to the sum of the rest of the phenotypes in F_2 of the parent family no. 92—19. This procedure should be followed generally, partly because of the avoidance of an unconscious selection in the taking out of the parent plants, which this procedure makes possible, partly because of the nullification of an eventual poor vitality of the double recessives.

The degree of the repulsion of this cross has been found to be 1 : 3,8 by means of the F_2-method, and the F_3-method gives the result

1 : 3,2. This must be considered a good correspondence in view of the standard error calculations. The value of n lies probably between 3 and 4 corresponding to the crossover percentage 25—20. On account of the numerical relations of the F_3-generation and the relatively good correspondence between the results of the coupling segregation as well as of the repulsion segregation it must be concluded that the value of n in all probability lies close to 3,5, which value corresponds to the crossover percentage 22,2.

The use of back crosses in the determination of the gametic ratio in *Lupinus angustifolius* is for many reasons technically difficult, as said before. The number of seeds in each pod is very limited, so a very great number of crosses had to be made to obtain sufficient quantities of seed. Numerous pollinations, in addition, do not succeed. At best, seeds from 4—5 flowers only are obtained, from each plant.

It may be of some interest to make a comparison between the precision and the practical advantages of the F_2- and F_3-methods, as similar conditions prevail in other genera, which have furnished important data with regard to linkage, as *Lathyrus, Triticum, Hordeum.* The F_3-method follows a more direct course, and the results would seem to be more reliable for this reason. This is particularly true in cases of repulsion, where the group of double recessives always is relatively small and consequently oftentimes doubtful. The association coefficient becomes uncertain in a corresponding degree. A fluctuation involving one or a few individuals may influence the ass. coeff. and displace the results considerably. The F_3-method offers great advantage in this respect as no attention need to be paid to the frequency of the numerically small groups. The advantage of this method is most clearly seen in cases where the number of the individuals in the recessive groups is decreased through poor vitality. MULLER made use of the F_3-method in *Drosophila* (1916, p. 354) in order to escape these difficulties. The advantage of the F_3-method is less obvious in the cross 9, just discussed, as the linkage here is relatively loose. It is better seen in cross 8 where close linkage is present, as already stated (pag. 316).

Although the F_3-method certainly is to be preferred, especially in case of a segregation of repulsion type, great practical difficulties may be encountered in the raising of a sufficient number of families necessitating much work and expense. It may therefore be of some interest to mention a short cut in the use of the F_3-method, which I intend

to employ in the future in *Lupinus*. It is labour-saving, and an analysis comprehensively enough may be made easier.

The difficulties in the raising of a sufficient number of F_3-families are remarkably reduced if the number of individuals in each family is intentionally decreased to a minimum. The question is to distinguish between the families segregating in the ratio 3 : 1 on the one hand, and the constant and the di-hybrids of different kinds on the other. A number of 32 individuals at the most in each family is required to make a sure discrimination — provided that the recessives are fully vital. The probability that a heterozygous plant shall give 32 dominants in succession is as 1 : 10000. Thus even if an analysis is made comprising up to 10000 families probably only one family would be found to be erroneously grouped. Such a wrong grouping is of no account, however, as the rarer family-group has occurred often, even in cases of close linkage. There is no need of so great a precision in the case of low or moderately high linkage values. If the number of individuals in the F_3-families are 24 throughout, one in 1000 families may be considered wrongly grouped. This precision may often be considered sufficiently accurate; indeed, a number of 20 individuals in each family will be sufficient in certain cases. The number of plants in each family may thus be limited to 20—32 according to conditions.

An F_3-analysis of such a great number of families may mean too great a work to many, even if the task has been made easier through the limitations proposed above. However, the number of the individuals may be still lowered in the following way. The sowing and the investigation of each family take place in different sets; only a few seeds of each family are sown the first time, for instance 4, the second portion may include another set of 4 seeds, and the rest, up to a maximum of 32 for instance, is sown the third time (if not a fourth set is tried). Families at once classed with certain segregating types — different in coupling and in repulsion — already at the first sowing do not need to be repeated in the sowings made later. The last sowing includes then mainly *one* of the two groups of segregating types together with a small number of segregates belonging to the other group, which by a chance failed to expose its place in the first sowings made. The extent of the work depends apparently on the number of families left for the last sowings. Much labour-saving may therefore be made if the parent plants of the F_3-families are selected in the appropriate way. From the checker scheme, fig. 2 a, it is at once seen that it is inexpedient to use simplex recessive F_2-

plants as parent plants in the case of repulsion. The majority of these are constants — the greater the repulsion, the greater their number — and the main part of the families from these plants would be left for the last sowing. Thus the simplex recessives should be excluded as parent plants in the case of repulsion; these should instead be taken from the duplex dominant group. The last sowing will then include only the 3:1-segregates, now in minority, together with the very few constant duplex dominants, and the di-hybrids, which have not yet shown their di-hybrid character. In the case of coupling, on the other hand, only the simplex recessive F_2-plants are selected; the experiment gets freed from the constant double dominants as well as from the families passing into repulsion. The total number of the individuals necessary in F_2 may be limited considerably in this way. Although seemingly paradoxical the statement holds true that the greater the coupling the easier the work, due to the fewness of the groups necessary in the last sowing.

The advantage of this procedure may be readily demonstrated by the following example. We assume that the gametic ratio in a case of repulsion, otherwise identical with cross 9, is 1 : 30 : 30 : 1. We assume, further, that F_2 segregates in 1000 blue, 500 violet and 500 bluish red for instance. The gametic ratio, then, is not to be found from the numerical relations in F_2; the F_3-analysis becomes necessary. As the fixing of the gametic ratio becomes surer the greater the number of families, 480 families for instance are raised. The following total number of plants has to be raised in the case of such an analysis. As it is a case of repulsion only blue individuals are used as parent plants. The constant blue group from the upper left corner of the periphery of the scheme and the groups passing into coupling, which groups in all represent the expectation $^3/_4$ family in a total of 480 families, are ignored. The families from the middle groups of the periphery, segregating in the ratio 3 : 1, have naturally to be included in the last sowing. Their number should be 30. The total number of individuals to be raised becomes 960, as 32 seeds from each of these 30 parent plants have to be sown successively. A number of 450 di-hybrid families, segregating 1 : 2 : 1, has further to be expected. The first sowing of these will then include 1800 plants in all. According to probability 43 % of these families will show their di-hybrid character, while 57 % have to be sown again. This makes 256 families and 1024 plants. When the result is combined with the numerical relations obtained in the first sowing 65 % of these 256 families are found to

be di-hybrids. Thus only 90 families are left for the third sowing. As 4 plants from each family have to be sown 360 plants are needed. At least 90 % of these 90 families must be assumed to have showed di-hybrid segregation (the figure has not been determined exactly as the results of the previous sowings have to be considered, which complicate the calculations), and only 9 such families have not yet been identified. The remaining 20 seeds from each family are now sown. The maximum number, 32, is reached, increasing the total with 180 plants. The following summarizes the results.

30	families	segregating	3 : 1,	each	with	32	individuals....		960	plants
1	sowing	of	450	di-hybrid	families,	each	with	4	individuals	1800 »
2	»	»	256	»	»	»	»	4	»	1024 »
3	»	»	90	»	»	»	»	4	»	360 »
4	»	»	9	»	»	»	»	20	»	180 »
									Total	4324 plants

The total number of plants becomes less, viz. 3790, in the case of coupling where the distinction is to be made between the constant and the 3:1-segregating families, and where only simplex. recessive plants are taken as parent plants.

If $^1/_2$ blue, $^1/_4$ violet and $^1/_4$ bluish red had been selected according to the numerical relations in F_2 instead of following the procedure just discussed a number of 9000 or 10000 plants had to be raised. If the number had been limited to 32 plants only in each family, and, furthermore, if parent plants had been grown from every phenotypic group without any portioning out of the investigation on different sowings a number of 15360 had to be raised.

In the case of a repulsion of 1 : 30 only one double recessive is expected in about 4000 individuals, which is just about the number required according to the F_3-method. This shows clearly the advantage of the F_3-method compared to the F_2-method. That it also advantageously competes with the back-cross method is seen from the fact that about 1000 plants had to be raised to secure a fixing of the gametic ratio with the same degree of accuracy. The raising af such a great number of hybrids must be considered a heavy task in the case of poor seeders and difficult pollination.

It is clear that the above procedure saves much labour, and that an F_3-analysis of sufficient extent is made easier. This must be of great value in cases where back crossing is difficult or impossible to perform on a large scale as, for instance, in the families Leguminosae

and Graminae, which are at the same time among the best studied with regard to genetics. Of course, the method has less value in many cases, as for instance in coupling between homomeric factors, in case of poor vitality on the part of recessives, in the event of a marked decrease in the germination power of the seeds when stored for sowings in successive years. It is capable of doing good service, however, when discriminatively used.

The result of the observations as to the seed colour in cross 9 remains to be stated. All isolated plants in F_2 and F_3 have been examined with regard to this point, and the colour of the flower has been noted at the same time. All blue and bluish red plants, amounting to 179 and 67 respectively, had earth-brown seeds, and all violet and pure red plants, amounting to 68 and 2 respectively, had rust-brown seeds. This agrees with the assumption that the rust-brown seed colour depends on the same factor as the pure red flower colour (factor *R*), and that the addition of the factor for violet colour (*V*) does not influence this seed colour, which remains rust-brown even when the flower colour passes into violet. It also agrees with the assumption that the earth-brown seed colour is caused by the *B*-factor when the fundamental factor *R* is present at the same time, while it is quite independent of the presence or absence of the *V*-factor. The assumed correlation between the seed colour and the flower colour is further strengthened by the fact that all families, constant with regard to pure red flowers in F_3 and F_4, also showed constancy with regard to rust-brown seed colour. The constant violets and the families segregating in violets and pure reds were also constant as to the rust-brown seed colour. Only a small number of families, however, were examined in this respect. In addition numerous cases have been investigated although not listed, and the correlation in question has been found to hold true in every case.

Cross 10 (tables 25—26).

Bluish red (*RRBBvvFF*) × tinged blue flower colour (*RRBBVVff*): no difference in seed colour.

F_1 was slightly diluted blue.

F_2 gave the following result:

	77 blue :	32 ting. blue :	41 bluish red :	6 ting. red
expected acc. to 9:3:3:1	$87{,}_{75}$	$29{,}_{25}$	$29{,}_{25}$	$9{,}_{75}$
D/M	$10{,}_{75}/6{,}_2 = 1{,}_{73}$	$2{,}_{75}/5{,}_4 = 0{,}_5$	$11{,}_{75}/5{,}_4 = 2{,}_{18}$	$3{,}_{75}/3 = 1{,}_{25}$

The result is quite normal with regard to the appearance of expected phenotypes as, contrary to the results obtained in cross 8, a dilution type of the fully coloured parent type (bluish red) originates. The numerical relations, however, do not agree well with the ratio 9 : 3 : 3 : 1. The discordance is still greater in F_3, which gives the following di-hybrid segregation numbers.

	277 blue	:	121 ting. blue	:	102 bl. red	:	7 ting. red
expected acc. to 9:3:3:1	285,3		95,1		95,1		31,7
D/M	$8{,}3/11{,}2 = 0{,}74$		$25{,}9/8{,}8 = 2{,}94$		$6{,}9/8{,}8 = 0{,}78$		$24{,}7/5{,}5 = 4{,}49$

The deficit in the tinged red group is remarkably great, and the deviation does not lie within the allowed range. The deviations become more appreciated when the di-hybrid segregations in F_2 and F_3 are summed up:

	354 blue	:	153 ting. blue	:	143 bl. red	:	13 ting. red
expected acc. to 9:3:3:1	372,9		124,3		124,3		41,4
D/M	$18{,}9/12{,}8 = 1{,}48$		$28{,}7/10{,}0 = 2{,}87$		$18{,}7/10{,}0 = 1{,}87$		$28{,}4/6{,}1 = 4{,}66$

There is a deficit in the blue and the tinged red groups, while there are too many in the tinged blue and in the bluish red groups. It is, therefore, very probable that we here have another case of repulsion, even if an ordinary di-hybrid Mendelian segregation with irregular segregation numbers would explain the matter. The great deficit in the recessives should then be traced back to poor vitality, although nothing else favours this assumption. Unfortunately, the analysis has not been carried out on a scale sufficient to guarantee a definite decision. The relatively small number of F_3-families due to diseases, which happened to damage the F_2-plots of this cross more than other plots, is particularly to be deplored. Otherwise the question could have been easily settled especially through the occurrence of families showing segregation characteristic of »coupling». It is true, one family has probably to be referred to this type, viz. no. 287—19, but the small number of individuals precludes a decision. The results of the segregation are by no means conclusive but some of the facts agree well with the assumption of the existence of repulsion in this cross, and this is further strengthened by the fact that each of the factors in question are coupled with a third to be discussed in the following.

The degree of the linkage is seen from table 4. A scrutiny of the reliability of these figures — in view of the relation between the

TABLE 4.

Reference number	Generation	Frequency of phenotypes VF	vF	Vf	vf	Total	Ass. coeff. of observed phenotypic ratio	Standard error M	Ass. coeff. of calcul. phenotypic ratio	Gametic ratio	Percentage of crossingover
						Repulsion.					
1	F_2	77	32	41	6	156	0,4792	0,1878	0,4752	1 : 1,8	35,7
2	F_3	249	119	96	5	462	0,8034	0,0837	0,8074	1 : 3,6	21,7
3	$F_2 + F_3$	326	151	137	11	625	0,7046	0,0827	0,7063	**1 : 2,7**	**27,0**
						Coupling.					
4	F_3	28	2	6	2	38	0,6470	0,3188	0,6407	2,3 : 1	33,3

zygotic groups to be expected in case of di-hybrid numbers in general, according to the facts stated on pag. 318 — at once shows that the numerical relations of nos. 1, 2 and 4 are very doubtful. The inner groups are rather unequal in all three cases, and the proportions between the outer terms are also irregular. The relations between $VF - (vF + Vf)$ and vf are listed in the following and compared to the relations to be expected at the numbers secured by the summing up of these two quantities.

1. $4 : 6 = 10$ expected $7{,}5 : 2{,}5$
2. $34 : 5 = 39$ » $29{,}25 : 9{,}75$
4. $20 : 2 = 22$ » $16{,}5 : 5{,}5$

The irregularities of the repulsion values in F_2 and F_3 become smoothed out when summed up, and the numerical relations (ref. no. 3) representing the sum of the repulsion values of both generations agree rather satisfactory with the general values just listed. The gametic ratio obtained from the summed up values is 1 : 2,7. The standard error of the association coefficient of the observed values in ref. no. 3 is 0,0826, which indicates a fluctuation of the gametic ratio between 1 : 2,3 and 1 : 3,4, or — if the threefold standard error is used — between 1 : 1,8 and 1 : 8. The uncertainty is thus seen to be very great. The deviations obtained between the different values of the gametic ratio lie within the allowed range.

The determination of the gametic ratio according to the F_3-method gives the following result. The number of families of different segregating types are listed in table 5; they are grouped in the same way

TABLE 5.

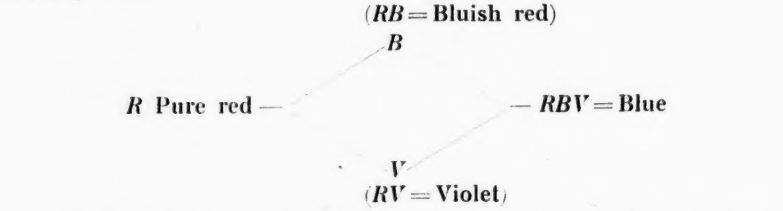
List of the number of families of different segregation types in F_3 from cross 10.

Colour of parent plant	Kinds of phenotypes in the families	Type of segregation	$4n^2$	$8n$	other groups
	Repulsion.				
Blue	Blue	Constant	—	—	2
»	Blue + bluish red + ting. blue + t. red	Coupling	—	—	1
»	» » » »	Repulsion	10	—	—
»	» + tinged blue	3 : 1	—	1	—
»	» + bluish red	3 : 1	—	4	—
Tinged blue	Tinged blue	Constant	2	—	—
»	» + tinged red	3 : 1	—	2	—
Bluish red	Bluish red	Constant	2	—	—
»	» + tinged red	3 : 1	—	1	—
Tinged red	Tinged red	Constant	—	—	1
			14	8	4

as in the previous cross. The equation in this case is found to be $\frac{14}{8} = \frac{n}{2}$; thus $n = 3{,}5$ corresponding to c. o. % 22,2. It is doubtful whether the results of the F_2-method or of the F_3-method shall be taken as decisive, as the number of F_2-families is rather small, as said before.

DISCUSSION OF THE FACTORIAL SCHEME.

The factorial scheme has been mentioned in short already on pag. 306; I shall discuss it more fully here. One factor, *R*, has been denoted for the anthocyan colour pure red, and two factors, *B* and *V*, for the transferring of this colour into bluish red and violet respectively; they change further the red ground colour into deep blue when both present.



There is, further, a factor for full flower colour; »diluted» forms originate when this factor is absent.

Cross 9 shows that the meeting of the factors *B* and *V* is necessary if deep blue colour shall result. Bluish red has been crossed here with violet, and F_1 is blue. The one type alone can not have carried the determiners of the blue colour as this colour is dominant over bluish red as well as over violet; these must have been distributed in the both parent types. The assumption of quite other factors than those for bluish red and violet bringing about the synthesis would also explain the matter, and the mere occurrence of a blue coloured F_1-generation in this cross is no adequate proof. The segregation in F_2 and F_3 would then have been another, however. Bluish red and violet individuals are found in the same number in F_2, and violets never originate from bluish reds in F_3, or vice versa. Plants of these colours never carry more than one of the determiners in question; the flower is always blue in the plants carrying both determiners. Thus this colour does not depend on a specific factor; it is on the contrary a compound character genetically, and the factors involved are the ones denoted for bluish red and violet.

The effect of these factors, on the other hand, depends on the factor for pure red or *R*. The *B*-factor induces a faint blue coloration in the red flower, as well as in the brownish red vegetative parts of the pure red type. It is apparently a bluing factor. It is another example of a factor with bluing effect in red flowers so commonly found in widely different genera. An examination of the bluish red flowers seems to show, however, that the red pigment has been transformed into blue pigment only in a limited number of cells. The red ground colour remains unchanged to a great extent, and only certain parts are more or less covered with a blue tinge. The bluish red colour, then, is not a specific colour but a combination of blue and red. It seems questionable only for this reason if it is to be compared with the purple colour in *Lathyrus*, for instance, a parallel which lies close at hand. The blue coloration spreads more diffusely in the flower with age, and the similarity with purple colour becomes greater. That the *B*-factor is a bluing factor is clearly seen in its relation to the seed colour. It has been assumed that the purpose of the *B*-factor with regard to seed colour is to transfer the rust-brown pigment of the pure red type into earth-brown. The examination of immature seeds shows, however, that the effect in fact also here is a blue coloration. Seeds still enclosed in the yellow but not yet dry pods show a red-violet coloration of the coloured parts in the rust-brown type, while the same parts in the earth-brown type are

blue. While the bluing effect of the *B*-factor is rather weak in the flowers, requiring the co-operation of the *V*-factor in order to produce the deep blue colour, no such co-operation is required in the case of the seeds. Blue seed colour is found in bluish red plants as well as in quite blue plants, and the colour has the same intensity in both cases; it is not possible to tell the particular type of flower colour from the colour of the seeds.

The *V*-factor transfers the pure red flowers colour into violet. It is not a question of a mixing in this case, apparently; the ground colour is probably wholly transferred into a new pigment. It is true that a faint tinge of blue is sometimes found also here, but the ground is always violet and not red. The *V*-factor does not influence the seed colour, and the rust-brown colour remains therefore quite unchanged.

It is of great interest to draw a parallel between the flower colours of different species and genera even if the accuracy of such a parallel becomes doubtful for want of chemical investigations. The studies of WILLSTÄTTER in the chemistry of the flower colours have showed a remarkable correspondence in the composition of the pigments in different genera. It appears very probable that the flower colour of *Lupinus,* although not analyzed chemically, presents similarities with numerous genera investigated by WILLSTÄTTER as to the composition of the pigments. The colour scale of *Lupinus* corresponds exactly with the scale found in *Centaurea* and *Delphinium;* the assumption of a correspondence as well in the chemistry of the pigments between *Lupinus* and the latter genera does not seem to be too bold.

The following points of comparison between the genetical scheme found in *Lupinus* and the chemical scheme of WILLSTÄTTER would then be held forth. The *R*-factor in the pure red type would be made responsible for the occurrence of acid cell sap and for the presence of the anthocyanin in the form of a homologue to the oxonium salt, which has been found to form the red pigment in *Centaurea.* The *V*-factor would cause a basic influence on the cell sap neutralizing the acid of the pure red type and liberating the anthocyanin, which now gives violet colour. The *B*-factor would also cause basic effect, as the blue colour found with this factor and caused by a calcium salt with the anthocyanin as a base requires alkaline cell sap. The *B*-factor alone, however, produces alkaline cell sap only in some of the cells of the flower. The result is a blue tinge on red ground, which gives rise to the compound colour bluish red. It seems quite natural

that the deep blue colour is the result of the co-operation of the two factors *B* and *V*, as both factors seem to cause alkalinity and as, further, the effect of the *V*-factor apparently pervades the whole flower. It is, indeed, of great interest that the neutral colour violet genetically is an intermediate between red and blue, between acid and alkaline colour. However, the schematic outline of the hypothesis of WILLSTÄTTER has its limitations; it was found that the red pigment of the rose-coloured form of *Centaurea* was not a cyanin variety, although expected, but a related still different pigment called pelargonin. This shows that the generalization made in the above must be looked upon with reservation.

A genetical analysis of a plant with similar colour scale has not yet been made, so far as I know. Deep blue colour together with violet and red do not occur, as a rule, in the plants more fully investigated in this respect (*Antirrhinum, Matthiola, Mirabilis, Papaver* etc.). In other cases a variety is found to be blue, being in these cases recessive, and not the type (*Lathyrus, Phlox, Anagallis*). The phenotypic difference between *Lupinus* and the latter genera would answer to the lack on the part of these of one link in the factorial chain of *Lupinus*. Purple in *Lathyrus* would correspond either to bluish red or violet in *Lupinus*, and *Lathyrus* would lack one or the other of the *Lupinus* factors *B* and *V*, which explains the absence of the blue compound form *BV*.

The necessity of assuming a fundamental factor for the appearance of colour on the whole is seen from crosses 6 and 7. White has been crossed in both these crosses with bluish red and violet respectively. F_1 is blue in both cases. With the knowledge of the constitution of the blue colour in mind the white parent plant must be assumed to have had at least one of the complementary factors for blue colour. We have, then, to assume that the white colour was due to the absence of a fundamental factor necessary for the development of bluish red as well as of violet, and thus also of the blue colour. Cross 5, white $\times$ tinged blue, favours also the idea of such a fundamental factor. However, it is not necessary to explain the blue colour in F_1 in this way. The tinged blue parent has indeed all determiners for blue colour and lacks only the full colour factor, which is introduced, however, by the white parent. It would be possible to assume that the white parent was devoid of all colour factors, and that it showed white colour because of this circumstance and not because of the absence of a fundamental factor only. The segregation in F_2, however, would then have

turned out differently and brought forth violet as well as bluish red plants. This is not the case. Only blue, tinged blue and white are present, and this shows that the white parent had all determiners for blue colour, while the necessary fundamental factor was absent. It has been assumed that the colour factor for pure red or *R,* which remains when the factors for bluish red and violet have been eliminated, should represent the fundamental factor just discussed. This is in accordance with all the results of the segregations, as pure red is the first link in the colour chain and as no indication of complementary fundamental factors has been obtained so far. The genus *Lupinus* would then form an exception similar to *Pisum,* as the presence of *two* fundamental factors has been found to be the rule in most genera carefully investigated. The most probable thing is, however, that two fundamental factors are present in these as well as in other genera, although only one has been established because of the use of whites lines, where only one of the factors, and always the same, has been present.

That this is so in *Lupinus* becomes very probable when it is remembered that only few lines of the genus have been investigated; my crosses comprise only two white flowered lines. That the same state of things has been found in the classic genus *Pisum* is a fact of greater significance. The diverging genetical constitution may indicate a deviating course of the formation of the colour. It would therefore be of great interest to follow up this side of the matter through an extensive study of white flowered lines of both genera.

The white colour in *Lupinus* shows another peculiarity, which distinguishes it from several other plants. The white forms of *Lupinus ang.* do not represent pure albino forms as is generally the case, in *Lathyrus* and *Antirrhinum* for instance. Certainly, they lack every trace of colour in all vegetative parts just as these, and buds and young flowers are pure white. Indeed, even older flowers may lack colour in certain cases. The flowers become coloured with age as a rule, however, and this coloration is sometimes very marked. Furthermore, the seeds of the white type are generally faint brown marbled with a rust-brown scar at the hilum. The same coloration of the seeds is found in *Pisum,* which also has »ghoast» coloured white seeds. Observations made the last year show that the shade of the colour is not the same in all whites, but varies with the colour factors present in a »latent» state. The outer conditions have apparently greatly favoured the development of the colour this year (unsui-

table weather conditions during the early vegetative season kept the young plants small and poorly developed for a long time). The distinct development of the colour made it easy to notice the difference in F_3 of cross 7 between the whites in the families segregating in blue and white, and the whites in the families segregating bluish red and white. The former were more bluish than the latter. A classification of the different white types coexisting in families of di-hybrid segregation was then tried. 62 white individuals from such families were divided in two groups. In the first group individuals were put having the same colour as the one noted in the families segregating in blue and white; the second group includes whites coloured in the same shade as in families segregating in bluish red and white. The numbers of individuals in these groups were 41 : 21; the expected proportions, according to the ratio 3 : 1, is 46,5 : 15,5. Thus it is clear that the factors *B* and *V* also determine the colour of the white types.

The question now becomes of interest whether the phenotypical differences between the white types in *Lupinus* and other genera indicate a difference as well in the factorial constitution. It is possible that the modifying factors *B* and *V* have a colour effect of their own without the co-operation of the fundamental factor. It is also possible that the white type does not represent an albino form but a dilution form, brought into existence by the absence of a full colour factor. These hypotheses are probably both erroneous. The colouration in question certainly does not indicate a diverging factorial constitution; it depends rather on purely physiological peculiarities. The coloration of the white flower belongs probably to the same category of phenomena as the shading of the colour noticeable in the coloured types in *Lupinus* when old. In the genus *Anchusa,* where also the colour of the flowers changes with age, no coloration of the white type is seen. Thus there are marked differences between the white types of *Lupinus* and of *Anchusa;* it does not invalidate, however, the parallel drawn in the above with regard to the shading of the coloured and white types. It is probably due to physiological changes in the tissues of the plant. A change in the permeability of the vacuolar membrane suggests itself. It is conceivable that a substance entering the vacuole may be endowed with the power to change the anthocyan of the cell sap, thus compensating the colour factor, which has been found to be absent. If we, accepting WHELDALE's hypothesis of colour formation, assume the presence in the white type of a factor for chromogen and the absence of the factor for the development of

oxydase in the cell sap no difficulty is met with in explaining the old age coloration through the entrance into the vacuole of a protoplasmatic oxydase, which in co-operation with the vacuolar chromogen develops the colour. (Cp. the hypothesis formulated by JONES with regard to the coloration of white types, JONES 1913, ref. in SCHIEMANN 1915). The following facts, however, should be noted. The shade of the old age coloration depends on the nature of the modifying factors present (*B* and *V*), as said before. WHELDALE regards the effect of the modifying factors as a continued oxidation of the products of the primary oxidation through specific enzymes. Such enzymes must therefore in this case have been present in the cell sap of a white plant with the constitution *rBV*, for instance. Thus these enzymes would not be able to compensate the enzyme of the fundamental *R*-factor; this should be attained, however, by a foreign enzyme (the *R*-factor is absent), which enters the vacuole — a rather strange phenomenon.

This hypothesis of the changes in the permeability of the vacuolar membrane agrees also with the interpretation of the nature of the white types given by SCHIEMANN. This is based on the facts established by WILLSTÄTTER that the anthocyan colours have a tendency to form colourless isomeres, and that certain substances have a power to check this isomerisation. The cell sap would then be assumed to contain anthocyan but of its colourless isomeric variety. A regeneration of the coloured isomere would be made possible through the successive changes in the chemical composition of the cell sap, provided that the above discussed changes in the permeability of the vacuolar membrane take place.

The above hypothesis is mentioned only as an example. Several other circumstances with similar effect may be conceived of as factors in the colour development of the flower. Furthermore, the change in the composition of the cell sap may just as well be accomplished through the withdrawal of a substance. It appears probable, however, that the development of colour in the white types follows this course or a similar one.

In the scheme proposed the *F*-factor has been assumed to have a general effect. It has also been assumed that the occurrence of diluted forms of the colours, determined by the presence of the other factors, is due to the absence of this *F*-factor. Dilution of blue has been found in all crosses, where dilution forms have been found at all, and full coloured blue has always been found at the same time

(crosses 4, 5, 8 and 10). That the *F*-factor also influences the bluish red colour (*RRBB*) is seen from cross 10, where tinged red originates as a product of recombination. It is true, no tinged form of violet has yet been found, but this is probably due to close linkage. It is, therefore, a difficult task to succeed in obtaining this form from the material at hand, although probably not unrealizable. The relation of the *F*-factor to the pure red factor is not yet known.

I have succeeded in determining the *Ff*-plants in the case of blue colour, as all F_1-generations involving the *F*-factor have showed a weak dilution of the blue colour. This dilution is so weak, however, that it is observed only in an F_1-plot, where all plants have the same diluted shading contrasting with the next, fully coloured plot. However, great difficulties are experienced in separating the different types in

TABLE 6.

Colour of parent plant		*FF*		*Ff*	
		Constant blue	Mono-hybrid, without dil.	Di-hybrid segregation	Mono-hybrid, without dil.
Blue.....	cross 5	7	6	4	1
	cross 10	2	4	5	0
	total	9	10	9	1
Sligthly diluted blue	cross 5	0	0	6	2
	cross 10	0	0	6	1
	total	0	0	12	3

F_2, where homo- and heterozygotically blue individuals are mixed. They have been listed with the pure blue type for this reason, when examined. I have classified the individuals as accurately as possible in blue and slightly diluted blue in the taking out of the parent plants for the F_3-families in crosses 5 and 10. The relation between the phenotype and the genotype in this case is shown in table 6. The result is significant. Individuals with the full colour factor in duplex stage have in no case been listed as slightly diluted blue but always as blue, but the *Ff*-individuals have been listed in 10 cases as blue and in 15 cases as slightly diluted blue. Presuming complete dominance of the *F*-factor these facts would be explained by the assumption that the *FF*-plants do not become modified towards diluted blue, while the *Ff*-individuals do become modified in this way. If the *F*-factor predominates only, the facts become explained by the

assumption that the colour of the *Ff*-plants may be intensified towards full blue colour. That is to say that the *Ff*-stage is more modifiable and therefore varies more than the *FF*-stage. Thus the transition to the *Ff*-stage is noticeable, though the main part of the colour dilution is due to the complete absence of the *F*-factor. This is true only of the blue colour, however, but not of the bluish-red type. I have not yet been able to distinguish the *vvFf*-types from the *vvFF*-types in spite of careful observations. The case of incomplete dominance mentioned is the only one found in *Lupinus;* the dominance is complete as to all other characters to all seeming.

The pleiotropic effect of the colour factors have already been mentioned; they give rise to coloration not only in the flowers but also in the sepals, in the cotyledons, in the axis etc. The *R*- and *B*-factors also influence the colour of the seed. The phenomenon is very common. WHELDALE cites 14 different genera, where a genetical connection between flower colour and anthocyan in vegetative parts has been found; they do not all represent pleiotropic phenomena, however. Among these genera intensifying factors and full colour factors have been found in *Antirrhinum* and *Primula,* and these factors influence also the coloration of the vegetative parts. I have not been able to find any data as to the eventual weakening of the colour in the leaf axils in *Lathyrus,* when the full colour factor is absent; this is the case in *Pisum,* however. A weakening of the colour of the flower is probably in most cases followed by a weakening of the colour of the vegetative parts. This is not the case in *Lupinus,* however. While the absence of the *F*-factor gives rise to a very marked dilution of the flower colour, which almost disappears in the beak of the keel, no trace of such a dilution is found in the vegetative parts of the plant. The faint coloured tinged red type has just as dark earth-brown seeds as the deep blue coloured type, and the colour of the bracts is identical with the colour of the bracts in the full coloured bluish red type. Thus a factor regulating the colour intensity of another pleiotropic factor influences the effect of this factor to different degrees in different organs. In one organ, e. g. the beak of the keel, every trace of the colour disappears although normally coloured intensively; in another organ no change in the colour is seen in spite of the fact that the colour often is very weak in the full coloured type, for instance in the stem, where only a faint tinge of colour covers the green ground. In still other organs, e. g. standard and wings, the

colour is weakened. The full colour factor, then, is not pleiotropic to the same degree as the colour factors.

Another interesting point of some weight has been mentioned with regard to the pleiotropism of the colour factors, which illustrates the common phenomenon that the effect of a pleiotropic factor differs in different organs. Two different cases of pleiotropism may be found. In the first case the factor has the same effect in different organs; blue colour in the flower as well as in vegetative parts as in *Lupinus,* and zygomorphism in both calyx and corolla as in *Antirrhinum,* according to BAUR, are good examples of this first kind. In the second case the effect of the factor varies in different degrees in different organs. Many examples are known of this kind, as for instance blue flower colour and earth-brown seed colour (*Lupinus*), and the flower colour and the width of the petals (TAMMES in *Linum*) to mention a more surprising case. The terms *isophene* and *heterophene pleiotropism* are proposed for these two kinds of pleiotropism. The isophene pleiotropism is clear enough but the heterophene kind present sometimes very unexpected combinations. However, the above mentioned case of heterophene pleiotropism in *Lupinus* (blue flower colour and earth-brown seed colour) is as readily explained as the isophene pleiotropism. When the immature seed is examined it is seen, as said before, that the earth-brown coloration induced by the factor *B,* really is a blue coloration, which passes into the earth-brown colour in consequence of maturing processes. In this case a morphological observation suffices to show that the means of action of the pleiotropic factor are the same in the both organs; the cause of the different phenotypical effects of the factor is wholly due to different conditions prevailing in the both organs. Another illustrative example of this kind of pleiotropism is the interpretation given by HERIBERT-NILSSON to account for the cracked bark and the curved leaves of certain segregates of *Salix*-bastards; both these characters are traced back to an abnormal rate of growth of the vascular cylinder (the xylem). A careful anatomical, physiological or chemical analysis of marked heterophene pleiotropism shall probably in many cases similarly bring out the fact that the differences are to be traced back to a common cause. The phenotypical diversity, of course, is due to one and the same undifferentiated genetical factor in these cases. As long as the real nature of the factors is unknown, there is no use of discussing the question, whether the genetical factor should be assumed to be undifferentiated and simple in the case of characters showing gene-

tical affinity but not yet proved to be related physiologically or chemically. It is, naturally, of great importance to know if the morphological effect of the one and same factor is due to circumstances conditioned by different developmental stages of the plant, different conditions prevailing in the different organs of the plant, or, on the contrary, if the factor itself is differentiated in some way. Thus the study of pleiotropic phenomena becomes of great weight when the nature of the genetical factors is brought under consideration.

THE SEED COLOUR.

The observations made with regard to the seed colour have been stated in the above in connection with the flower colours; they have been assumed to arise from the same factors due to the pleiotropic nature of these factors. The results of the segregations agree also throughout with this interpretation; they allow also the assumption, however, that specific seed colour factors are closely coupled with the flower colour factors. This is, however, very uncertain, even if certain facts would seem to point in this direction, as for instance the fact the *V*-factor, as well as the full colour factor, do not influence the seed colour. The evidence obtained, however, does not support the giving up of the assumption made, that the flower colour factors also determine the colour of the seeds.

There is one character of the seed colour, however, that has not yet been treated, viz. the marbling. Two types differing in the distribution of the pigment have been described on pag. 303. The earth-brown and the rust-brown colour are either marbled or evenly distributed to full intensity over the whole surface of the seed, with the exception for small distinct white flecks. The marbling is brought about by the scattered distribution of the pigment grains in flecks of irregular form and extent. The colour of these flecks is gray, and small white flecks also occur here. Marbling dominates over non-marbling, and F_2 segregates in the ratio 3 : 1. In cross 2, the only cross where the non-marbled variety has been used, the following results have been obtained:

215 marbled : 63 non-marbled

expected : 208,5 69,5 $D/M = \frac{6,5}{7,22} = 0,9.$

The weakening of the colour, which is characteristic of the gray flecks, does not involve an intensifying of the colour in the marbled

areas, which would have been expected had the quantity of the pigment been the same and only the distribution of it unequal. The non-marbled type has exactly the same intensity of colour as the marbled areas of the other type. Thus it is clear that the marbled form is a type weaker in colour than the non-marbled variety. This is of a certain interest, as the marbled type dominates over the non-marbled, according to the results obtained. Thus the *M*-factor, assumed to be responsible for the marbling, exhibits the character of an inhibiting factor. Its effect, however, is limited to the seed; it has no weakening effect on the flower. The marbling factor operates probably quite independent of the flower colour factors. Earth-brown and rust-brown segregate in cross 2 in addition to the marbling character. The di-hybrid segregation is quite normal, and the following values have been obtained:

162 earth-brown, marbled : *47* earth-brown, non-marbled : *53* rust-brown, marbled : *16* rust-brown, non-marbled.

expected	156,4	52,1	52,1	17,4
D/M	$=\frac{5,6}{8,3}=0,67$	$\frac{5,1}{6,5}=0,78$	$\frac{0,9}{6,5}=0,14$	$\frac{1,4}{4,0}=0,35.$

DISCUSSION OF THE LINKAGE CASES.

The results of the analysis have proved that linkage occurs in two crosses (crosses 8 and 9); the third case of linkage is not absolutely proven (cross 10, bluish red × tinged blue). The factors involved are *B, V* and *F*. The factors coupled in cross 8 are *B* and *F*, in cross 9, *B* and *V*. In cross 10 the factors *V* and *F* are segregating; linkage is thus to be expected also in this case, and the results of the segregation go to show that this view is correct. They do not offer any proof when considered separately, but the fact that each of the factors involved is coupled with a third is conclusive. This being so, theory and the results obtained claim coupling between *V* and *F* as well; the results of the segregation agree well with this assumption, and coupling must be considered proven between the factors *V* and *F*. The factors *B, V* and *F* are then situated in the same chromosome, according to the chromosome theory, and their location is assumed to be the following.

According to cross 8 there is very close linkage between the factors *B* and *F*, as in a large material no crossovers (tinged violet) have been obtained. Furthermore, it is very improbable that a continued

analysis of this cross shall establish a crossover percentage higher than 2 %. It will probably be found that the percentage does not exceed 1 %; it will rather fall below this figure, as the chances of a crossover percentage more or less than $^1/_3$ % are equal, as shown on pag. 316. The factors *B* and *F* are then situated in the closest proximity to each other. According to cross 9 there is linkage between *B* and *V* to a degree corresponding to a crossover percentage of about 22 %. The F_2-analysis gives the value 20,4, and the F_3-analysis 23,8. The same crossover percentage is to be expected between the factors *V* and *F* on account of the closeness between the factors *B* and *F*. The values obtained in the case of *V*—*F* are 27 % according to the F_2-analysis, but 22,2 % according to the F_3-analysis. The F_3-result shows thus a striking correspondence with the expectation.

The location of the factors *B*, *V* and *F* in the chromosome may then be demonstrated in the following way.

It should be stated that the mutual location of the proximate factors *B* and *F* is rather gratuitous. All crosses have shown that the fourth flower colour factor, the pure red factor *R*, operates independent of the other factors; it is probably situated in another chromosome. The same is probably true of the marbling factor, which has been shown to be independent of the *B*-factor. The relation of the *M*-factor to the fundamental factor *R* is not yet known.

The coupling between the factors *B* and *V* is particularly interesting. The linkage between these factors is very close; it is perhaps complete, as no crossovers have been found. This might favour the supposition that the present case should be interpreted as a case of multiple allelomorphs. This is erroneous, however, as seen below. The factor denotation used by MORGAN has been adopted in the following presentation of the facts. In order to avoid confusion with the presence-absence system previously employed, only large letters have been used; commas and ¯symbols have been used as indices of mutations (see MORGAN 1915 pag. 219).

BV = blue, wildtype; BV' = violet; $B'V$ = bluish red; $B'V'$ = pure red; BV^- = tinged blue; $B'V^-$ = tinged red.

It should be observed that violet colour, for instance, is here called V^-contrary to the presence-absence indices, where violet is denoted, *V*, while *v* denotes bluish red.

According to the above symbols the non-appearance of the tinged violet type in F_2 of cross 8 (tinged blue $\times$ violet) should depend on the fact that the factor producing the dilution of the blue colour and the factor responsible for the violet colour, denoted V^- and V' respectively, are different allelomorphs of the same wildtype factor V. Already the F_1-result of this cross invalidates this assumption. If correct, no synthesis of the wildtype would be obtained from the cross $BV' \times BV^-$; this synthesis was secured, however.

Another supposition is: that the wildtype factor B, which produces bluish red flower colour when mutating into B', also should give rise to B^- and B'^- mutations causing the formation of tinged blue (B^-V) and tinged red (B'^-V), is likewise out of question. The non-appearance of tinged violet should then depend on the fact that the V-factor did not mutate in an analogous way. The synthesis of blue in the cross bluish red $\times$ tinged blue ($B'V \times B^-V$) would not be obtained in the case of such a factor construction.

The present case of coupling can not be interpreted as a case of multiple allelomorphs, as seen; it is linkage, and it is perhaps complete.

It is very difficult to determine, however, whether the linkage is partial or complete. The non-appearance of the crossovers may be explained by assuming a corresponding displacement of the linkage value, and the comprehensiveness of the analysis cannot alone decide the matter. Indeed, it is doubtful whether there is such a condition as complete linkage. The term becomes superfluous if only the closest partial linkage conceivable is considered. The question becomes another if the assumption is made that two factors are able to lie side by side in the same chromomere without excluding each other as multiple allelomorphs. The term complete linkage would then imply a definite meaning distinguished from partial linkage, and essentially different from multiple allelomorphism. There is nothing in point of principle to say against such an assumption, as the idea of the chomomeres only expresses the belief of the breaking up of the chromosomes into their constituent elements. The chromomeres represent the smallest parts of division of the chromosomes, which does not imply, however, that they each carry only one factor.

Some of the essential facts of the inheritance of the flower colour and of the seed colour in *Lupinus angustifolius* have now been presented. The definite fixing of the linkage values, the precise relation of the marbling factor to the other factors, and the complete analysis

of the poly-hybrid segregations are facts of interest still uninvestigated. In the crosses analyzed, comprising about 800 families and 27000 individuals, segregation with regard to earliness was also found. The most surprising uniformity prevailed in flowers as well as in vegetative parts for the rest. It is true, the colour of the seed varies remarkably with regard to the intensity and the distribution. The variations are, no doubt, only modifications, as the colour of the seed is very sensitive to environmental conditions. New mutations have not been observed.

On this occasion I wish to express my sincerest thanks to Mr. H. WEIBULL, director of the plant breeding institute at Weibullsholm, Landskrona, for his great kindness of promoting these studies in different ways.

SUMMARY.

1) Seven different types of flower colours and five types of seed colours have been genetically analyzed.

2) One fundamental colour factor has been demonstrated (pure red). A synthesis of blue colour has been obtained from crosses between bluish red and violet flower colours. One »dilution» factor has been found to be present.

3) Pleiotropic correlation has been demonstrated between certain flower and seed colours.

4) Three flower colour factors have been found to form a linkage group. The linkage between two of the factors is very close, if not complete. The other linkage value represent a crossover percentage of about 22 %.

5) The importance of the »F_3-analysis» in the determination of the linkage values in cases where back crossing is technically difficult has been demonstrated.

6) A method, that greatly facilitates the carrying out of the F_3-analysis, has been proposed.

7) The colour scale blue-violet-red (blue as the wildtype), now investigated genetically, is phenotypically analogous with the colour scale in the genus *Centaurea* a. o. chemically analyzed by WILLSTÄTTER.

TABLE 7. *F_2 of the cross white × blue n:r 1.*

Colour of parent plant	Field-number	Blue	White	Total
Blue	592—18	81	23	104
»	593—18	35	8	43
»	594—18	47	18	65
»	595—18	85	16	101
»	596—18	41	8	49
	Total	289	73	362

TABLE 8. *F_2 of the cross violet × blue n:r 2.*

Colour of parent plant	Field-number	Blue	Violet	Total
Blue	3339—17	57	19	76
»	3340—17	44	19	63
»	3341—17	9	3	12
»	3342—17	47	14	61
»	3343—17	58	18	76
	Total	215	73	288

TABLE 9. *F_3 of the cross violet × blue n:r 2.*

Number of parent family	Colour of parent plant	Field-number	Blue	Violet	Total
3339—17.....	Blue	578—18	22	—	22
3340—17.....	Blue	581—18	35	14	49
	»	582—18	60	23	83
	»	583—18	14	2	16
3342—17.....	»	584—18	111	39	150
	»	585—18	60	27	87
	»	586—18	73	17	90
	»	588—18	41	16	57
	»	589—18	62	16	78
		Total	456	154	610
3340—17.....	Violet	579—18	—	129	129
	»	580—18	—	43	43
3342—17.....	»	587—18	—	75	75
		Total	—	247	247

TABLE 10. *F_2 of the cross bluish red × blue n:r 3.*

Colour of parent plant	Field-number	Blue	Bluish red	Total
Blue	610—18	28	5	33
»	611—18	61	25	86
»	612—18	22	5	27
»	613—18	11	5	16
	Total	122	40	162

TABLE 11. *F_3 of the cross bluish red × blue n:r 3.*

Number of parent family	Colour of parent plant	Field-number	Blue	Bluish red	Total
610—18	Blue	255—19	35	—	35
	»	257—19	33	—	33
611—18	»	267—19	75	—	75
	»	268—19	64	—	64
	»	269—19	23	—	23
612—18	»	276—19	37	—	37
		Total	267	—	267
	Blue	253—19	57	17	74
	»	254—19	44	18	62
	»	258—19	23	11	34
610—18	»	260—19	20	5	25
	»	261—19	38	8	46
	»	262—19	23	11	34
	»	263—19	36	13	49
611—18	»	271—19	55	18	73
		Total	296	101	397
610—18	Bluish red	264—19	—	20	20
	»	266—19	—	52	52
611—18	»	272—19	—	57	57
	»	273—19	—	34	34
	»	274—19	—	11	11
613—18	»	278—19	—	28	28
		Total	—	202	202

TABLE 12. *F_2 of the cross tinged blue × blue n:r 4.*

Colour of parent plant	Field-number	Blue	Tinged blue	Total
Slightly diluted blue	630—18	69	24	93
	631—18	57	21	78
	632—18	82	33	115
	633—18	117	34	151
	634—18	71	26	97
	Total	396	138	534

TABLE 13. *F_3 of the cross tinged blue × blue n:r 4.*

Number of parent family	Colour of parent plant	Field-number	Blue	Tinged blue	Total
630—18	Blue [1]	515—19	47	—	47
633—18	»	523—19	54	—	54
	»	527—19	33	—	33
634—18	»	533—19	52	—	52
	»	534—19	55	—	55
	»	538—19	41	—	41
		Total	282	—	282
630—18	Blue [1]	514—19	19	7	26
	»	516—19	36	9	45
	»	517—19	19	5	24
	»	518—19	21	11	32
631—18	»	519—19	27	8	35
633—18	»	524—19	34	8	42
	»	525—19	37	15	52
	»	528—19	35	12	47
	»	529—19	35	9	44
634—18	»	535—19	19	7	26
	»	539—19	42	16	58
		Total	324	107	431
632—18	Tinged blue	521—19	—	8	8
	»	522—19	—	17	17

[1] Because of the difficulty in separating the blue ones and the slightly dil. blue no record is made of the latter in this cross.

Number of parent family	Colour of parent plant	Field-number	Blue	Tinged blue	Total
633—18	Tinged blue	530—19	—	55	55
	»	531—19	—	4	4
634—18	»	541—19	—	15	15
	»	542—19	—	8	8
	»	543—19	—	35	35
	»	544—19	—	5	5
		Total	—	147	147

TABLE 14. *F_2 of the cross white × tinged blue n:r 5.*

Colour of parent plant	Field-number	Blue	Tinged blue	White	Total
Slightly diluted blue	3332—17	17	6	7	30
	3334—17	22	2	4	28
	3335—17	6	2	0	8
	3336—17	8	0	7	15
	Total	53	10	18	81

TABLE 15. *F_3 of the cross white × tinged blue n:r 5.*

Number of parent family	Colour of parent plant	Field-number	Blue	Tinged blue	White	Total
3332—17.....	Blue	512—18	20	—	—	20
	»	514—18	23	—	—	23
3334—17.....	»	530—18	54	—	—	54
	»	541—18	31	—	—	31
3335—17.....	»	544—18	42	—	—	42
	»	545—18	37	—	—	37
3336—17.....	»	551—18	54	—	—	54
		Total	261	—	—	261
3332—17.....	Blue	516—18	17	3	4	24
	»	517—18	15	5	5	25
	»	519—18	15	5	6	26
	?[1]	527—18	17	10	4	31
3334—17.....	?	528—18	31	13	15	59
	Sl. dil. blue	529—18	11	8	5	24
	»	531—18	26	11	8	45
	»	532—18	29	10	14	53
	»	536—18	13	6	4	23
	Blue	539—18	50	10	23	83
	Sl. dil. blue	543—18	18	9	10	37

[1] Not recorded.

Number of parent family	Colour of parent plant	Field-number	Blue	Tinged blue	White	Total
3335—17.....	?	547—18	45	14	13	72
3336—17.....	Sl. dil. blue	552—18	50	23	27	100
		Total	337	127	138	602
3332—17.....	?	509—18	23	3	—	26
	Sl. dil. blue	511—18	38	12	—	50
3334—17.....	?	526—18	15	10	—	25
	Sl. dil. blue	533—18	43	9	—	52
	Blue	540—18	20	6	—	26
3336—17.....	?	548—18	19	8	—	27
		Total	158	48	—	206
3332—17.....	Blue	518—18	18	—	4	22
3334—17.....	»	534—18	61	—	20	81
	»	538—18	39	—	13	52
	»	542—18	33	—	11	44
3336—17.....	»	550—18	38	—	14	52
	»	553—18	35	—	16	51
		Total	224	—	78	302
3332—17.....	Tinged blue	503—18	—	34	—	34
	»	508—18	—	54	—	54
3334—17.....	»	523—18	—	27	—	27
3335—17.....	?	546—18	—	68	—	68
3336—17.....	?	549—18	—	33	—	33
		Total	—	216	—	216
3332—17.....	Tinged blue	504—18	—	36	15	51
	»	505—18	—	19	6	25
	»	506—18	—	61	20	81
	»	507—18	—	17	3	20
3334—17.....	»	524—18	—	46	12	58
		Total	—	179	56	235
3332—17.....	White	501—18	—	—	15	15
	»	502—18	—	—	25	25
		Total	—	—	40	40

TABLE 16. *F_2 of the cross violet × white n:r 6.*

Colour of parent plant	Field-number	Blue	Violet	White	Total
Blue	3337—17	4	3	1	8
»	3338—17	23	13	7	43
	Total	27	16	8	51

TABLE 17. *F_3 of the cross violet × white n:r 6.*

Number of parent family	Colour of parent plant	Field-number	Blue	Violet	White	Total
3338—17.....	Blue	556—18	35	10	14	59
	»	558—18	33	6	7	46
	»	559—18	15	1	10	26
	»	561—18	44	23	19	86
	»	562—18	89	36	42	167
		Total	216	76	92	384
3338—17.....	Blue	557—18	56	28	—	84
	»	560—18	25	6	—	31
	»	565—18	25	6	—	31
	»	568—18	29	10	—	39
		Total	135	50	—	185
3338—17.....	Blue	563—18	48	—	16	64
	»	564—18	48	—	13	61
	»	566—18	54	—	10	64
	»	567—18	19	—	4	23
		Total	169	—	43	212
3338—17.....	Violet	572—18	—	74	—	74
	»	573—18	—	54	—	54
	»	574—18	—	98	—	98
		Total	—	226	—	226
3337—17.....	Violet	554—18	—	15	8	23
3338—17.....	»	570—18	—	53	16	69
	»	571—18	—	68	31	99
	»	575—18	—	81	23	104
	»	576—18	—	25	15	40
		Total	—	242	93	335
3338—17.....	White	577—18	—	—	36	36

TABLE 18. *F_2 of the cross bluish red × white n:r 7.*

Colour of parent plant	Field-number	Blue	Bluish red	White	Total
Blue	545—19	10	3	4	17
»	546—19	31	12	13	56
	Total	41	15	17	73

TABLE 19. *F_3 of the cross bluish red × white n:r 7.*

Number of parent family	Colour of parent plant	Field-number	Blue	Bluish red	White	Total
546—19	Blue	338—20	42	—	—	42
	»	345—20	51	—	—	51
		Total	93	—	—	93
	Blue	342—20	22	7	8	37
	»	346—20	17	7	7	31
	»	348—20	18	2	7	27
	»	354—20	20	9	10	39
	»	355—20	23	5	10	38
		Total	100	30	42	172
	Blue	337—20	17	9	—	26
	»	347—20	16	5	—	21
		Total	33	14	—	47
	Blue	344—20	33	—	13	46
	»	352—20	14	—	11	25
		Total	47	—	24	71
	Bluish red	358—20	—	21	—	21
	»	359—20	—	36	—	36
	»	360—20	—	25	—	25
	»	363—20	—	35	—	35
		Total	—	117	—	117
	Bluish red	361—20	—	33	7	40
	White	228—20	—	—	7	7
	»	229—20	—	—	8	8
	»	231—20	—	—	21	21
	»	232—20	—	—	17	17
	»	233—20	—	—	14	14
	»	234—20	—	—	15	15
	»	236—20	—	—	12	12
		Total	—	—	94	94

TABLE 20. *F_2 of the cross tinged blue × violet n:r 8.*

Colour of parent plant	Field-number	Blue	Violet	Tinged blue	Total
Slightly diluted blue	618—18	14	11	14	39
	619—18	32	12	13	57
	620—18	31	24	18	73

Colour of parent plant	Field-number	Blue	Violet	Tinged blue	Total
Slightly diluted blue	621—18	16	7	12	35
	622—18	45	29	30	104
	623—18	75	31	38	144
	624—18	44	14	17	75
	625—18	53	19	26	98
	626—18	50	21	33	104
	627—18	26	16	10	52
	628—18	32	34	19	85
	629—18	52	23	25	100
	Total	470	241	255	966

TABLE 21. *F_3 of the cross tinged blue × violet n:r 8.*

Number of parent family	Colour of parent plant	Field-number	Blue	Violet	Tinged blue	Total
619—18	Blue	329—19	23	8	7	38
	»	330—19	34	15	18	67
	»	331—19	9	5	11	25
620—18	»	336—19	15	11	9	35
	»	339—19	19	13	14	46
621—18	»	346—19	43	12	15	70
	»	347—19	28	20	14	62
	»	348—19	25	12	16	53
	»	349—19	38	18	8	64
	»	350—19	39	12	20	71
	»	351—19	14	5	11	30
	»	355—19	23	12	17	52
	»	356—19	25	6	11	42
	»	357—19	14	6	8	28
	»	359—19	21	12	11	44
	»	360—19	28	17	17	62
	»	361—19	34	25	9	68
622—18	»	381—19	15	3	7	25
	»	384—19	22	14	9	45
	»	387—19	21	4	12	37
	»	389—19	25	13	9	47
	»	390—19	22	8	11	41
	»	391—19	18	7	9	34
	»	392—19	19	9	12	40
623—18	»	405—19	17	9	10	36
	»	409—19	7	3	10	20
	»	410—19	15	9	11	35
	»	411—19	15	11	12	38

Number of parent family	Colour of parent plant	Field-number	Blue	Violet	Tinged blue	Total
623—18	Blue	413—19	15	11	3	29
	»	414—19	25	3	2	30
	»	416—19	11	4	5	20
	»	417—19	16	13	7	36
	»	418—19	7	6	7	20
	»	419—19	14	12	10	36
	»	420—19	17	9	12	38
624—18	»	434—19	8	9	8	25
	»	436—19	12	7	9	28
	»	437—19	22	12	10	44
	»	438—19	19	7	10	36
	»	439—19	21	12	9	42
	»	440—19	17	10	9	36
	»	441—19	16	13	10	39
	»	442—19	20	8	12	40
	»	443—19	28	13	11	52
	»	444—19	7	7	12	26
	»	445—19	20	12	15	47
	»	447—19	11	3	7	21
625—18	»	465—19	16	10	11	37
	»	466—19	14	8	5	27
	»	467—19	16	5	6	27
	»	468—19	16	6	12	34
626—18	»	469—19	9	8	15	32
628—18	»	483—19	30	18	8	56
	»	490—19	15	9	2	26
	»	491—19	12	6	5	23
	»	492—19	20	11	3	34
629—18	»	498—19	16	9	12	37
	»	500—19	10	6	7	23
	»	501—19	29	8	10	47
	»	503—19	23	12	13	48
		Total	1,160	586	605	2,351
620—18	Violet	341—19	—	63	—	63
621—18	»	374—19	—	63	—	63
	»	376—19	—	39	—	39
	»	380—19	—	30	—	30
622—18	»	394—19	—	37	—	37
	»	395—19	—	56	—	56
623—18	»	421—19	—	33	—	33
	»	422—19	—	38	—	38
	»	423—19	—	37	—	37
	»	424—19	—	49	—	49
	»	425—19	—	45	—	45

Number of parent family	Colour of parent plant	Field-number	Blue	Violet	Tinged blue	Total
623—18	Violet	426—19	—	33	—	33
	»	448—19	—	44	—	44
624—18	»	449—19	—	58	—	58
	»	450—19	—	38	—	38
	»	452—19	—	50	—	50
625—18	»	472—19	—	20	—	20
626—18	»	484—19	—	38	—	38
628—18	»	493—19	—	24	—	24
	»	495—19	—	43	—	43
629—18	»	506—19	—	22	—	22
	»	507—19	—	56	—	56
		Total	—	916	—	916
618—18	Tinged blue	327—19	—	—	20	20
620—18	»	344—19	—	—	34	34
	»	345—19	—	—	33	33
621—18	»	362—19	—	—	62	62
	»	369—19	—	—	55	55
	»	370—19	—	—	73	73
	»	371—19	—	—	34	34
	»	372—19	—	—	34	34
	»	373—19	—	—	47	47
622—18	»	396—19	—	—	42	42
	»	397—19	—	—	36	36
	»	399—19	—	—	24	24
	»	400—19	—	—	30	30
	»	401—19	—	—	42	42
	»	402—19	—	—	37	37
	»	403—19	—	—	25	25
	»	404—19	—	—	42	42
623—18	»	428—19	—	—	24	24
	»	429—19	—	—	29	29
	»	430—19	—	—	40	40
	»	431—19	—	—	38	38
	»	432—19	—	—	27	27
	»	433—19	—	—	35	35
624—18	»	455—19	—	—	40	40
	»	456—19	—	—	48	48
	»	457—19	—	—	22	22
	»	458—19	—	—	49	49
	»	459—19	—	—	36	36
	»	460—19	—	—	44	44
	»	461—19	—	—	34	34
	»	462—19	—	—	39	39
	»	463—19	—	—	35	35

Number of parent family	Colour of parent plant	Field-number	Blue	Violet	Tinged blue	Total
624—18	Tinged blue	464—19	—	—	30	30
625—18	»	473—19	—	—	39	39
	»	474—19	—	—	54	54
	»	475—19	—	—	66	66
	»	476—19	—	—	26	26
	»	477—19	—	—	31	31
	»	479—19	—	—	20	20
626—18	»	486—19	—	—	33	33
628—18	»	496—19	—	—	55	55
	»	497—19	—	—	26	26
629—18	»	509—19	—	—	30	30
	»	512—19	—	—	42	42
		Total	—	—	1,662	1,662

TABLE 22. *F_2 of the cross bluish red × violet n:r 9.*

Colour of parent plant	Field-number	Blue	Violet	Bluish red	Pure red	Total
Blue	597—18	55	24	18	5	102
»	598—18	38	14	16	—	68
»	599—18	27	12	9	—	48
»	600—18	14	5	3	—	22
»	601—18	18	6	9	—	33
»	602—18	27	14	12	1	54
»	603—18	62	27	27	—	116
»	604—18	15	9	6	1	31
»	605—18	64	43	27	2	136
»	606—18	77	30	35	4	146
»	607—18	30	20	20	1	71
»	608—18	67	45	23	—	135
»	609—18	62	20	21	1	104
		556	269	226	15	1,066

TABLE 23. *F_3 of the cross bluish red × violet n:r 9.*

Number of parent family	Colour of parent plant	Field-number	Blue	Violet	Bluish red	Pure red	Total
598—18 ...	Blue	20—19	35	5	2	3	45
603—18 ...	»	73—19	37	4	5	13	59
605—18 ...	»	92—19	49	4	8	9	70
	»	96—19	39	8	10	14	71

Number of parent family	Colour of parent plant	Field-number	Blue	Violet	Bluish red	Pure red	Total
605—18 ...	Blue	112—19	49	5	2	10	66
607—18 ...	»	189—19	32	2	3	13	50
		Total	241	28	30	62	361
	Blue	16—19	26	17	19	—	62
	»	17—19	39	18	10	—	67
598—18 ...	»	18—19	32	18	12	1	63
	»	19—19	19	12	10	—	41
	»	24—19	24	5	12	—	41
	»	41—19	38	15	30	—	83
	»	44—19	21	2	5	—	28
601—18 ...	»	45—19	15	11	10	—	36
	»	46—19	26	15	8	2	51
	»	47—19	28	19	16	—	63
602—18 ...	»	55—19	25	7	9	—	41
	»	65—19	28	18	20	—	66
	»	66—19	19	6	10	—	35
603—18 ...	»	68—19	15	5	6	—	26
	»	74—19	30	14	11	1	56
604—18 ...	»	84—19	29	17	13	2	61
	»	90—19	32	8	18	—	58
	»	93—19	27	17	16	—	60
	»	99—19	28	10	17	1	56
	»	100—19	11	8	5	—	24
	»	104—19	45	10	12	—	67
605—18 ...	»	105—19	30	18	17	—	65
	»	107—19	30	17	17	1	65
	»	108—19	22	14	13	—	49
	»	113—19	15	8	15	—	38
	»	115—19	13	4	8	1	26
	»	154—19	25	13	5	—	43
	»	156—19	7	8	10	—	25
	»	164—19	14	7	3	—	24
606—18 ...	»	165—19	27	15	14	1	57
	»	166—19	41	9	18	—	68
	»	168—19	38	12	14	1	65
	»	169—19	35	15	18	3	71
607—18 ...	»	190—19	32	15	6	—	53
	»	201—19	45	17	12	1	75
	»	203—19	35	15	12	1	63
608—18 ...	»	204—19	28	17	15	1	61
	»	205—19	29	15	18	1	63
	»	207—19	30	14	10	—	54
	»	212—19	7	4	9	—	20
609—18 ...	»	237—19	31	15	13	2	61

Number of parent family	Colour of parent plant	Field-number	Blue	Violet	Bluish red	Pure red	Total
609—18 ...	Blue	239—19	28	25	14	—	67
	»	241—19	23	11	12	—	46
		Total	1,142	540	542	20	2,244
598—18 ...	Blue	23—19	34	10	—	—	44
	»	25—19	73	27	—	—	100
603—18 ...	»	64—19	52	13	—	—	65
	»	71—19	19	6	—	—	25
605—18 ...	»	95—19	39	6	—	—	45
	»	97—19	46	5	—	—	51
	»	110—19	35	15	—	—	50
	»	119—19	38	9	—	—	47
606—18 ...	»	158—19	18	6	—	—	24
	»	161—19	24	3	—	—	27
	»	162—19	36	17	—	—	53
	»	167—19	55	15	—	—	70
	»	172—19	20	6	—	—	26
607—18 ...	»	193—19	17	4	—	—	21
	»	194—19	33	15	—	—	48
608—18 ...	»	202—19	18	13	—	—	31
609—18 ...	»	238—19	33	15	—	—	48
	»	242—19	29	4	—	—	33
		Total	619	189	—	—	808
599—18 ...	Blue	33—19	39	—	13	—	52
	»	34—19	28	—	9	—	37
600—18 ...	»	36—19	66	—	36	—	102
601—18 ...	»	43—19	23	—	11	—	34
603—18 ...	»	67—19	28	—	11	—	39
	»	72—19	37	—	16	—	53
605—18 ...	»	91—19	27	—	8	—	35
	»	98—19	42	—	8	—	50
	»	101—19	48	—	6	—	54
	»	102—19	46	—	14	—	60
	»	103—19	25	—	11	—	36
	»	106—19	36	—	11	—	47
	»	109—19	39	—	16	—	55
	»	118—19	36	—	9	—	45
606—18 ...	»	157—19	30	—	16	—	46
	»	159—19	54	—	17	—	71
	»	160—19	30	—	12	—	42
608—18 ...	»	206—19	28	—	15	—	43
609—18 ...	»	240—19	33	—	10	—	43
		Total	695	—	249	—	944

Number of parent family	Colour of parent plant	Field-number	Blue	Violet	Bluish red	Pure red	Total
602—18 ...	Violet	57—19	—	59	—	—	59
	»	58—19	—	20	—	—	20
	»	59—19	—	43	—	—	43
	»	60—19	—	63	—	—	63
603—18 ...	»	75—19	—	72	—	—	72
604—18 ...	»	86—19	—	58	—	—	58
605—18 ...	»	121—19	—	79	—	—	79
	»	122—19	—	54	—	—	54
	»	132—19	—	60	—	—	60
	»	133—19	—	22	—	—	22
	»	136—19	—	63	—	—	63
	»	137—19	—	67	—	—	67
	»	138—19	—	54	—	—	54
	»	140—19	—	68	—	—	68
	»	141—19	—	45	—	—	45
606—18 ...	»	176—19	—	23	—	—	23
	»	177—19	—	37	—	—	37
607—18 ...	»	196—19	—	42	—	—	42
608—18 ...	»	214—19	—	51	—	—	51
	»	216—19	—	68	—	—	68
	»	218—19	—	47	—	—	47
	»	219—19	—	22	—	—	22
	»	221—19	—	81	—	—	81
	»	222—19	—	54	—	—	54
	»	223—19	—	77	—	—	77
	»	227—19	—	44	—	—	44
609—18 ...	»	244—19	—	66	—	—	66
	»	245—19	—	52	—	—	52
		Total	—	1,491	—	—	1,491
600—18 ...	Violet	39—19	—	56	—	18	74
601—18 ...	»	48—19	—	24	—	11	35
	»	49—19	—	39	—	10	49
605—18 ...	»	120—19	—	52	—	21	73
	»	123—19	—	53	—	21	74
	»	128—19	—	40	—	12	52
	»	129—19	—	47	—	19	66
	»	131—19	—	24	—	4	28
	»	134—19	—	31	—	16	47
	»	135—19	—	37	—	14	51
	»	139—19	—	18	—	6	24
606—18 ...	»	174—19	—	26	—	8	34
607—18 ...	»	195—19	—	30	—	10	40
608—18 ...	»	213—19	—	45	—	10	55

Number of parent family	Colour of parent plant	Field-number	Blue	Violet	Bluish red	Pure red	Total
608—18 ...	Violet	217—19	—	45	—	14	59
	»	220—19	—	53	—	10	63
609—18 ...	»	224—19	—	43	—	12	55
	»	247—19	—	16	—	4	20
		Total	—	679	—	220	899
598—18 ...	Bluish red	29—19	—	—	60	—	60
	»	32—19	—	—	69	—	69
601—18 ...	»	51—19	—	—	76	—	76
	»	61—19	—	—	34	—	34
602—18 ...	»	62—19	—	—	39	—	39
	»	63—19	—	—	31	—	31
	»	78—19	—	—	63	—	63
	»	79—19	—	—	94	—	94
603—18 ...	»	82—19	—	—	73	—	73
	»	83—19	—	—	47	—	47
604—18 ...	»	88—19	—	—	23	—	23
	»	142—19	—	—	71	—	71
	»	144—19	—	—	55	—	55
	»	146—19	—	—	39	—	39
605—18 ...	»	148—19	—	—	28	—	28
	»	149—19	—	—	33	—	33
	»	150—19	—	—	54	—	54
	»	151 19	—	—	54	—	54
	»	152—19	—	—	63	—	63
	»	178—19	—	—	37	—	37
	»	179—19	—	—	53	—	53
606—18 ...	»	181—19	—	—	69	—	69
	»	186—19	—	—	51	—	51
	»	187—19	—	—	65	—	65
607—18 ...	»	197—19	—	—	29	—	29
	»	228—19	—	—	49	—	49
	»	231—19	—	—	60	—	60
608—18 ...	»	234—19	—	—	66	—	66
	»	236—19	—	—	57	—	57
	»	250—19	—	—	58	—	58
609—18 ...	»	251—19	—	—	68	—	68
	»	252—19	—	—	61	—	61
		Total	—	—	1,729	—	1,729
598—18 ...	Bluish red	28—19	—	—	58	14	72
599—18 ...	»	35—19	—	—	35	12	47
603—18 ...	»	80—19	—	—	15	7	22
	»	81—19	—	—	34	6	40
605—18 ...	»	143—19	—	—	40	14	54

Number of parent family	Colour of parent plant	Field-number	Blue	Violet	Bluish red	Pure red	Total
605—18 ...	Bluish red	145—19	—	—	49	20	69
	»	147—19	—	—	30	10	40
606—18 ...	»	180—19	—	—	55	11	66
	»	182—19	—	—	29	13	42
607—18 ...	»	200—19	—	—	17	6	23
608—18 ...	»	229—19	—	—	55	10	65
	»	230—19	—	—	47	17	64
609—18 ...	»	249—19	—	—	43	17	60
		Total	—	—	507	157	664
605—18 ...	Pure red	153—19	—	—	—	10	10
606—18 ...	»	188—19	—	—	—	63	63
		Total	—	—	—	73	73

TABLE 24. *F_4 of the cross bluish red × violet n:r 9.*

Number of parent family	Colour of parent plant	Field-number	Blue	Violet	Bluish red	Pure red	Total
92—19	Blue	299—20	22	1	4	2	29
	»	301—20	26	8	4	2	40
	»	302—20	22	3	4	6	35
	»	312—20	23	2	2	3	30
	»	315—20	27	2	4	4	37
	»	319—20	25	1	4	5	35
	»	321—20	18	5	5	1	29
	»	322—20	23	5	4	4	36
	»	326—20	18	1	1	6	26
		Total	204	28	32	33	297
	Blue	324—20	9	8	3	—	20
92—19	Blue	303—20	22	—	—	—	22
	»	309—20	32	—	—	—	32
	»	310—20	23	—	—	—	23
	»	314—20	24	—	—	—	24
	»	316—20	46	—	—	—	46
	»	317—20	50	—	—	—	50
		Total	197	—	—	—	197
	Blue	292—20	29	5	—	—	34
	»	300—20	21	5	—	—	26
	»	313—20	30	9	—	—	39
	»	318—20	19	2	—	—	21
		Total	99	21	—	—	120

Number of parent plant	Colour of parent plant	Field-number	Blue	Violet	Bluish red	Pure red	Total
92—19	Blue	311—20	19	—	9	—	28
	»	325—20	20	—	6	—	26
		Total	39	—	15	—	54
	Violet	327—20	—	24	—	—	24
	Violet	328—20	—	20	—	6	26
	Bluish red	330—20	—	—	31	—	31
	»	331—20	—	—	21	—	21
	»	332—20	—	—	60	—	60
	»	335—20	—	—	47	—	47
		Total	—	—	159	—	159
	Bluish red	334—20	—	—	18	5	24

TABLE 25. *F_2 of the cross bluish red × tinged blue n:r 10.*

Colour of parent plant	Field-number	Blue	Tinged blue	Bluish red	Tinged red	Total
Slightly diluted blue	614—18	8	11	8	2	29
	615—18	22	9	12	2	45
	616—18	47	12	21	2	82
	Total	77	32	41	6	156

TABLE 26. *F_3 of the cross bluish red × tinged blue n:r 10.*

Number of parent family	Colour of parent plant	Field-number	Blue	Tinged blue	Bluish red	Tinged red	Total
616—18 ...	Blue	303—19	26	—	—	—	26
	»	305—19	38	—	—	—	38
		Total	64	—	—	—	64
615—18 ...	Blue	286—19	18	6	10	—	34
	»	287—19	28	2	6	2	38
616—18 ...	»	298—19	38	15	9	—	62
	»	299—19	16	6	4	1	27
	»	301—19	29	18	13	—	60
	Sl. dil. blue	306—19	28	14	15	—	57
	»	307—19	35	23	17	3	78
	»	309—19	21	8	9	—	38
	»	312—19	21	6	7	—	34
	»	313—19	9	8	4	1	22
	»	315—19	34	15	8	—	57
		Total	277	121	102	7	507

Number of parent family	Colour of parent plant	Field-number	Blue	Tinged blue	Bluish red	Tinged red	Total
616—18 ...	Sl. dil. blue	311 –19	66	19	—	—	85
614—18 ...	Blue	279—19	22	—	9	—	31
615—18 ...	»	288—19	20	—	5	—	25
616—18 ...	»	302—19	19	—	5	—	24
	»	304—19	17	—	6	—	23
		Total	78	—	25	—	103
615—18 ...	Tinged blue	291—19	—	22	—	—	22
	»	293—19	—	43	—	—	43
		Total	—	65	—	—	65
616—18 ...	Tinged blue	316—19	—	48	—	21	69
	»	317—19	—	60	—	24	84
		Total	—	108	—	45	153
616—18 ...	Bluish red	318—19	—	—	33	—	33
	»	322—19	—	—	51	—	51
		Total	—	—	84	—	84
614—18 ...	Bluish red	283—19	—	—	14	6	20
615—18 ...	Tinged red	297—19	—	—	—	3	3

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SELEKTIVE VERSCHIEBUNG DER GAMETENFREQUENZ IN EINER KREUZUNGSPOPULATION VON ROGGEN

VON *NILS HERIBERT-NILSSON*

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WÄHREND meiner züchterischen Arbeit mit Roggen in Weibullsholm fand ich im Jahre 1913 unter den Nachkommenschaften einzelner Pflanzen eine (122—1913), die einen grossen Prozentsatz einer scharf abweichenden Variante zeigte. Sie war dadurch sehr auffallend, dass sowohl Stengel, Blätter als Ähren vollkommen ohne den sonst immer bei Roggen zu findenden Wachsüberzug waren, wodurch die Pflanzen ein wildgrasähnliches Aussehen erhielten. Die Stengel hatten ungefähr die dunkelgrüne Farbe von *Triticum repens*. In dem betreffenden Bestand wurden sämtliche bereiften Pflanzen vor der Blüte beseitigt, sodass die Kreuzung nur zwischen den unbereiften Pflanzen stattfand. Die Eigenschaft erwies sich im folgenden Jahre als konstant. Da der unbereifte Typus so selten ist, dass ich ihn während meiner züchterischen Arbeit nur zweimal gefunden habe und da er sonst nur einmal früher von VILMORIN angetroffen worden ist, da er ausserdem zu gewöhnlichem bereiftem Roggen rezessiv ist, habe ich ihn für sehr geeignet als Indikator bei Versuchen über den Vizinismus des Roggens gefunden. Über derartige Versuche habe ich schon berichtet (Zeitschr. für Pflanzenzüchtung 1917).

In dem erwähnten vor der Blüte auf wachsfreie Pflanzen selektionierten Bestand wurde bei der Reife eine Pflanze (122 b—13) wegen ihrer kurzen Halme als Elitepflanze ausgewählt, und die Körner dieser Pflanze wurden im Herbst in einem Weizenfeld von anderen Nachkommenschaften räumlich isoliert ausgesät. Da der Boden ungeeignet war, erhielt ich nur 5 Pflanzen. Später im Herbst wurde von einem Nachbar ein Roggenfeld nur 20 m von diesen Pflanzen entfernt ausgesät. Die Indikatorpflanzen wurden deshalb bei der Roggenblüte 1914 nicht nur unter sich, sondern auch von dem Felde mit gewöhnlichem, bereiftem Roggen bestäubt. Die Nachkommenschaft der Indikatorpflanzen ergab deshalb 1915 auf 39 Nachkommen 14 Vizinisten, die also aus Kreuzung mit dem Roggenfelde stammten.

Vor der Blüte wurden alle Indikatoren ausgemerzt. Nur die Vizinisten kreuzten sich also bei der Blüte. Diese repräsentierten die F_1 einer Kreuzung Indikator $\times$ Bereift, wo zwar die bereiften Väter wohl ebenso viele als die F_1-Pflanzen waren. Falls aber die Differenz eine monohybride wäre, würde ja dies keine Komplikation herbeiführen, sondern man könnte eine normale Spaltung in F_2 erwarten. Diese trat auch ein, indem F_2 aus 296 bereiften Pflanzen und 96 Indikatoren bestand. Da die Erwartung $294 : 98 \pm 8{,}57$ für eine monohybride Spaltung ist, ist die Übereinstimmung zwischen Gefundenem und Erwartetem sehr gut. Obgleich die Eltern sehr verschiedene habituelle Typen repräsentierten, indem die Indikatorpflanze eine feinhalmige und feinährige, schwachhalmige Pflanze aus dem Brattingsborgsroggen war, die Väter starkhalmige, grobährige und steifhalmige Pflanzen aus dem Petkuserroggen waren, und obgleich die Bereifung eine Eigenschaft ist, der oft grosse oekologische Bedeutung zugemessen wird, verläuft jedoch die Spaltung ganz regelrecht. Unter den Kulturverhältnissen scheint also die Bereifung, jedenfalls bei dem Roggen, keinen selektorischen Wert zu haben.

F_2

	A	a
A	AA	Aa
a	aA	aa

F_3

	A	A	a
A	AA	AA	Aa
A	AA	AA	Aa
a	aA	aA	aa

F_4

	A	A	A	a
A	AA	AA	AA	Aa
A	AA	AA	AA	Aa
A	AA	AA	AA	Aa
a	aA	aA	aA	aa

Spaltung: **3 : 1**

Gametenfrequenz nach der Eliminierung $= 4 : 2 = \mathbf{2 : 1}$

Spaltung: **8 : 1**

Gametenfrequenz nach der Eliminierung $= 12 : 4 = \mathbf{3 : 1}$

Spaltung: **51 : 1**

Gametenfrequenz nach der Eliminierung $= 24 : 6 = \mathbf{4 : 1}$

Die exakte Spaltung führte mich auf den Gedanken, einen rationellen Versuch mit Eliminierung der Rezessiven durch mehrere Generationen auszuführen, um festzustellen, ob die Zahlenverhältnisse mit den theoretisch zu berechnenden übereinstimmen würden. Nach Mendels Regel muss ja die Spaltungszahl der F_2 bei freier Durchein-

anderkreuzung des F_2-Bestandes in den folgenden Generationen konstant dieselbe bleiben, falls die verschiedenen Spaltungskomponenten gleich vital sind. Aber hieraus folgt auch, dass man die Spaltungszahl durch das Ausmerzen eines bestimmten Komponenten allmählich verschieben könnte. Denn durch die selektive Eliminierung z. B. der rezessiven Klasse wird die Gametenfrequenz zwischen Dominanten und Rezessiven in ein ganz neues Zahlenverhältnis überführt, was auch ein ganz neues aber konstantes Zahlenverhältnis in bezug auf die Spaltung der nächsten Generation verursachen muss.

Theoretisch muss ein Versuch mit allmählicher und vollständiger Eliminierung der Rezessiven einer monohybriden Spaltung in einem fremdbestäubenden Bestand so ausfallen, wie die Spaltungsquadrate S. 365 veranschaulichen.

Die Gametenfrequenz erhält man, weil die Homozygoten Gameten im Verhältnis 2 : 0, die Heterozygoten im Verhältnis 1 : 1 bilden, durch Summierung der beiden Allelomorphen je für sich, nach Abrechnen der rezessiven Kombination (in den Quadraten fett eingerahmt). Die Gametenfrequenz nach Eliminierung der Rezessiven in F_2 wird der Spaltungszahl der F_3 zu Grunde gelegt u. s. w. Diese Gametenfrequenz ist, wie aus den Spaltungsquadraten hervorgeht, in F_2 2 : 1, in F_3 3 : 1, in F_4 4 : 1 u. s. w. Die allgemeine Formel wird also für diese in einer bestimmten Generation n : 1. Die neuinduzierten Spaltungszahlen sind in F_3 8 : 1, in F_4 15 : 1 u. s. w. Aus diesen lässt sich die allgemeine Spaltungsformel $n^2 - 1 : 1$ berechnen.

Mein Versuch mit Eliminierung der Rezessiven hat dieses Jahr schon F_7 erreicht. Das Resultat ist in der Tabelle 1, S. 367 zusammengestellt worden. In der zweiten Kolumne sind die theoretischen Spaltungstypen jeder Generation angegeben, in der letzten Kolumne sind die entsprechenden Prozentzahlen für die rezessive Klasse angegeben, die eine bessere Übersicht des rein züchterischen Erfolgs des Versuches geben.

Aus der Tabelle geht hervor, dass die theoretisch berechneten Spaltungen auch sehr schön auftreten. Die Spaltungszahlen sind ganz auffallend gut, indem sie in keinem Falle ausserhalb des einfachen mittleren Fehlers fallen. Da die Spaltungspopulationen gross sind, müssen die Versuche als ganz einwandfrei betrachtet werden. *Die Versuchsreihe zeigt also, dass man durch suczessive Eliminierung der Rezessiven die Gametenproportionen verschieben und neue Spaltungszahlen induzieren kann, aber die Spaltung, die man laut Mendels Regel theoretisch erwarten muss, tritt bei der Gametenverteilung in der*

Population ebenso klar und exakt hervor wie bei der Gametenverteilung innerhalb einer selbstbestäubenden Pflanze. Aus dem Versuch geht die Konstanz der Gametenverteilung auch bei suczessiver Verschiebung der Gametenproportionen hervor. Natürlich wäre nichts anderes zu erwarten, und der Versuch ist deshalb nur eine experimentelle Bestätigung theoretischer Voraussetzungen, die aber, da sie als Grundlage der Züchtung fremdbestäubender Pflanzen betrachtet werden müssen, eine empirische Verifizierung wohl auch einmal brauchen. Man könnte ja meinen, dass wohl die Gameten in den theoretischen Verhältnissen an *jeder Pflanze für sich* gebildet werden, dass aber durch die modifikativ ungleiche Kräftigkeit der Pflanzen

TABELLE 1.

Spaltungszahlen nach suczessiver Rezessiveliminierung durch sechs Generationen des F_1-Bestandes 424—1915.

Deszendenz	Theoretisch erwarteter Spaltungstypus	Spaltungszahl					Prozent Rezessiver	
		Gefunden		Erwartet		Mittlerer Fehler	Gefunden	Erwartet
		mit Wachs	ohne Wachs	mit Wachs	ohne Wachs			
F_1	1 : 0	14	—	—	—	—	—	—
F_2	3 : 1	296	96	294	98	± 8,57	24,7	25,0
F_3	8 : 1	337	39	334,33	41,67	± 6,09	11,6	11,1
F_4	15 : 1	1273	88	1275,94	85,06	± 8,93	6,5	6,3
F_5	24 : 1	350	17	352,32	14,68	± 3,75	4,6	4,0
F_6	35 : 1	783	19	779,73	22,27	± 4,65	2,4	2,8
F_7	48 : 1	1313	24	1309,72	27,28	± 5,17	1,8	2,0

jedoch die Spaltungszahlen *des Bestandes* beträchtlich verschoben werden könnten. Mein Versuch zeigt, dass die grossen Schwankungen in bezug auf die Grösse der Pflanzen und folglich auch in bezug auf die Gametenproduktion, die in einem Bestand immer zu finden sind, sich jedoch ganz ausgleichen, jedenfalls falls die Bestände gross sind. Die Population spaltet ganz wie eine riesengrosse Pflanze.

Da ich 1916 noch nicht wusste, ob die Bestäubung des oben behandelten Indikatorbestandes von einheitlichen Vätern ausgeführt worden war, führte ich in diesem Jahre mit dem oben erwähnten Ziel auch eine artifizielle Kreuzung zwischen einer Indikatorpflanze und einer stark bereiften Pflanze aus der Weibullsholmerzüchtung Sturmroggen aus. Die letzterwähnte Sorte weicht von Petkuserrog-

gen, der bei der oben behandelten Kreuzung die Vaterpflanzen lieferte, durch kürzere und steifere Halme und etwas kürzere Ähren ab. Die Differenz zwischen Indikatorroggen und Sturmroggen ist noch grösser als zwischen Indikator und Petkuser. Das Ausfallen dieser Versuchsreihe, die dieses Jahr die F_5 erreicht hat, geht aus Tabelle 2 hervor.

Die Tabelle zeigt, dass auch in dieser Deszendenzserie die gefundenen Zahlenverhältnisse gut mit den theoretischen übereinstimmen. Zwar sind die Verhältnisse nicht so ausserordentlich schön wie in der oben erwähnten Serie, aber in keinem Falle gehen sie ausserhalb des doppelten mittleren Fehlers. Auch diese Spaltungen können deshalb

TABELLE 2.

Spaltungszahlen nach suczessiver Rezessiveliminierung durch vier Generationen des F_1-Bestandes 431—1917.

Deszendenz	Theoretisch erwarteter Spaltungstypus	Spaltungszahl					Prozent Rezessiver	
		Gefunden		Erwartet		Mittlerer Fehler	Gefunden	Erwartet
		mit Wachs	ohne Wachs	mit Wachs	ohne Wachs			
F_1	1 : 0	10	—	—	—	—	—	—
F_2	3 : 1	464	155	464,25	154,75	± 10,77	25,0	25,0
F_3	8 : 1	832	119	845,33	105,67	± 9,69	12,5	11,1
F_4	15 : 1	775	57	780	52	± 6,98	6,9	6,3
F_5	24 : 1	1481	50	1469,76	61,24	± 7,67	3,3	4,0

als ganz gesichert betrachtet werden und verifizieren noch stärker die Konstanz der Gametenverteilung bei suczessiver Eliminierung der Rezessiven. Auch die F_2 dieses Versuches zeigt, dass die Indikatoren, obgleich unbereift, ebenso vital wie die bereiften Roggenpflanzen sind. Natürlich ist es dann auch zu erwarten, dass die Indikatorheterozygoten vollkommen vital sein werden, wie auch die späteren Generationen demonstrieren.

Von züchterischem Gesichtspunkte ist es bemerkenswert, wie schnell der Prozentsatz an Rezessiven durch die Selektion in den ersten Generationen abnimmt. In F_3 ist er nur 11 % gegen 25 % in F_2, in F_4 nur 6 %, in F_7 2 %. In F_{10} ist er 1 %, aber dann fällt er fast unmerklich, sodass er in F_{20} noch 0,25 % ist. Während der ersten 10 Generationen fällt das Rezessivprozent also 24 %, während der

nächsten 10 Generationen nur 0,75 %. Aber schon nach 10 Generationen kann ein Bestand praktisch genommen als einheitlich betrachtet werden, speziell falls es mehr habituelle Differenzen wie Blatttypus oder Blattfarbe, Ährenform oder Ährenlänge und derartige Differenzen gilt. In diesem Falle hat man schon in F_5 ziemlich ausgeglichene Bestände. Bei mehr auffallenden Differenzen wie Schartigkeit und Halmlänge tut man besser, neue Elitepflanzen zu entnehmen und die Nachkommenschaften räumlich zu isolieren.

THE RACE PROBLEM OF THE ROMAN EMPIRE

BY *MARTIN P. NILSSON*
LUND

THE fall of the Roman Empire is the greatest tragedy of history. States have been wiped out and peoples crushed before and since, but the fall of the Roman Empire implied also the fall of the only great and world-wide culture that existed before that to which we belong. Humanity returned to much more primitive conditions of social and economic life, not to speak of education and culture.

Different causes of the rapid disappearance of the glory that was Rome have been sought for. They need not be discussed here. There is more than one cause, and it will be difficult and misleading to reduce them to a single and common formula. That there is also a problem of the biological order was first pointed out by Professor SEECK[1]. His views are an outcome of the typical popular Darwinism of the time in which he wrote. The cruelty and suspiciousness of the emperors removed and killed all persons who, by their mental qualities, capacity, and energy, raised themselves above the average. Through an artificial, inverted selection independence and originality were stamped out and a servile people bred. The possibility of such a process cannot be denied but to attain to any result it would have to be carried out on a large scale and over a protracted period, since the population of the Empire is considered to have amounted to about 100 millions[2]. Proportionally to this, the number of the victims of the emperors' cruelty was very small, and their extinction cannot have had any considerable effect on the stock of the population of the Empire. In reality the thesis of Professor SEECK cannot be maintained. But the problem is there, and I think that it can be approached more safely in the light of modern research.

There are great innate differences between the races of humanity: some have more natural ability than others. Sometimes it has been the fashion to deny this, and to contend that a people with all its peculiarities is the result of its environments, the *milieu,* and the

country. Facts show that this is manifestly erroneous. What was the American continent before its discovery, and what has it become since its occupation by the European peoples? The country around the Hebrus is much the same as that around the Axius, yet the Macedonians created a great empire, while the Thracians were hardly able to form a state at all, although HERODOTUS says that the Thracians and the Indians were the greatest peoples of his time. The natural features of Southern Italy and Sicily are very similar to those of Greece, but the original inhabitants of these countries created no culture; the Greeks brought it to them. The Greek people, not the Greek country, created the culture which is and ever will be the basis of Western civilization [3].

The hereditary dispositions of different races are very different, although we cannot yet grasp these distinctions in detail. There are hereditary dispositions of greater and lesser value. There are dispositions which enable a people to organize a state and create a culture. In ancient times the Greeks and the Romans did this, and only they on a large scale. They were the peoples that created ancient civilization and the Roman Empire; the fate of these depended on them.

I have not here to speak of civic problems or problems of culture. It is well known that the different rights of the inhabitants of the Empire were levelled down, and that the Greco-Roman culture spread throughout all the provinces. The question was whether the Romans were to raise the provincials to their level and assimilate them with themselves or to be assimilated by the provincials, which would include a levelling down of the culture. In the first two centuries the process was in general the former, in the later centuries it was inverted. With this we must not confound the superficial diffusion of the Latin language, which at last embraced the whole of western Europe. For a discussion of this question I refer to my forthcoming book on the Roman Empire [4], and turn now to the biological problem which lies at the basis of the problem of cultures.

If the Romans were to assimilate the provincials with themselves, the foremost condition was a sufficient multiplying of their numbers, i. e. a sufficiently high birth-rate. The Romans had once before carried through a similar task on a smaller scale — the Romanising of Italy. Roman colonies were spread throughout the whole country, the Roman people multiplied in numbers, the almost unlimited supply of soldiers from the colonies gave Rome the victory over the superior genius and strategy of HANNIBAL. After the Social war the kindred

Oscan-Umbrian tribes, and soon afterwards the Celts of the Po valley, were merged in the Roman nation and enlarged and invigorated it. The new task, the Romanising not of a single country but of the Empire, of a world, was gigantic and needed a proportionately increasing birth-rate.

But this scheme failed. We see in our own days how the fall of the birth-rate commences in the upper classes and soon spreads down to the lower. This decline seems to be common to all high culture, at least the same phenomenon appeared among the civilized populations of the Empire, the Greeks and the Romans. As to Greece the statements of POLYBIUS and PLUTARCH are well-known. POLYBIUS says, in the middle of the second century B. C., that childless marriages were common and that the population was diminishing, although neither pestilence nor war had checked the increase. PLUTARCH, at the end of the first century A. D., states that the whole of Greece would not be able to raise the 3,000 soldiers that the little town of Megara had sent to the battle of Salamis.

For Rome and Italy the testimony is abundant that the birth-rate declined during the earlier years of the Empire. In the country the decline reached back into the Republican age, and was connected with agrarian problems. The class of small farmers, from which Rome had once drawn her irresistible armies, was expelled by the formation of great estates cultivated by slaves. This is once of the best known features of that age.

The bonds of matrimony were slackened, the birth and education of children were felt to be burdensome. In ancient times the parents had a right to expose children whom they did not desire to educate. Where the supply of food is scarce among primitive peoples this may be excused. Among a civilized people, when economic egotism has obliterated the natural feelings of the parents, it is nothing but legalized infanticide. This stain on ancient culture, however, did not have any considerable influence on the number of the population. Most of the exposed babies were picked up by slave-hunters; they lived, though in the debased condition of slaves. A more important feature was that the educated classes were decimated in this manner. The ancients also knew other less revolting means of checking the birth-rate, the effect of which may safely be supposed to have been much greater. These expedients are often mentioned in the medical literature of the period, and many seem to have looked on them as some extreme feminists do to-day [5].

A curious circumstance shows how common childlessness was among the upper classes. This was the competition for inheritances, which the moralists satirized and thundered against in vain. It was not only a literary commonplace but a very real evil. The philosopher SENECA writes to a mother who had lost her only son that in these times childlessness contributes to the importance of a person rather than deprives him of it. Even the legislation was put in action against the annoyance [6].

Much more important are the legal means used to raise the birth-rate. The first emperor, AUGUSTUS, in spite of an embittered resistance, enacted the famous laws which enforced every Roman of noble birth between 25 and 60 years to be married, or at least engaged [7]. The irony of fate willed that both the consuls who gave the law their names were unmarried. Parents of three and more children had valuable prerogatives, especially in regard to the higher offices in the state. Unmarried persons were deprived of the privilege of visiting the circus and the theatres and could not receive legacies, childless legatees were deprived of half their inheritance. These means were more drastic than any that have been imagined in our times, but they were of no avail.

The decline of the birth-rate begins in the upper classes, and AUGUSTUS had perhaps thought that if it could be checked there the example would influence the lower classes. But he also tried to support poor families with a flourishing crowd of children. He used to present them with 1,000 sesterces for every child. An inscription of the small town of Atina in Latium recounts that a certain BASILA has given to the town a fund of 400,000 sesterces in order that the children of the inhabitants may receive corn for their food and at the age of puberty a sum of 1,000 sesterces each to set them up in life. This is the first example of the means by which the emperors later on tried to raise the birth-rate of the people in Italy. In reality it is liberating the parents from the cost of feeding the children and transferring this to public funds. The emperors NERVA and TRAJAN in particular carried out this scheme on a large scale, and patriotic private persons helped them with great gifts. PLINY the younger, for example, gave half a million sesterces to his native town of Comum for this purpose. The later emperors of the second century vigorously carried out the work and created a staff of supervising officers [8]. It must be acknowledged that those in authority recognized the evil and did their utmost to check it. In proportion to the finances of the

time, the use of these funds which were destined to raise the birth-rate of the Roman population is the greatest social measure that history records. It failed, however. In the hardships of the third century the funds diminished and finally disappeared.

In some cases it is possible to show whence the men came who took the places of the Roman elements of the population. The old Roman nobility had been severely dealt with in the proscriptions at the end of the Republic. AUGUSTUS tried earnestly to save what was left, but without success. The old families died out in the first century A. D. [9]. The correspondents of PLINY the younger do not bear the old famous names. In their stead provincials enter the senate, at first from the most Romanised provinces, Southern Spain (Baetica), South-East France (Gallia Narbonensis), later on from Africa (Tunis), and Asia Minor. The first consuls who originated from Spain appear in the last years of the Republic and were followed by several others during the first century A. D., the first consul from Gallia Narbonensis is found in the reign of TIBERIUS, the first from Africa and Syria in the reigns of VESPASIAN and DOMITIAN respectively. From TRAJAN onwards even the emperors were provincials. TRAJAN and his successor HADRIAN were Spaniards, ANTONINUS PIUS belonged to a Gallic and MARCUS AURELIUS to a Spanish family, SEPTIMIUS SEVERUS was a native of Africa, his successors were Syrians. It was difficult for a man belonging to the Greek portion of the Empire to attain a high position, because a knowledge of Latin and Roman law was needed for this, and such a knowledge was not common in the East, which prided itself on its own ancient culture. Nevertheless after the reign of HADRIAN numbers of Orientals appear in high places; the western world seems almost to be worn out.

The army was not great in proportion to the population of the Empire — in the first two centuries about 300,000 men, while the inhabitants of the Empire are considered to have amounted to 70—100 millions — but it played a very important part in the shifting of the population. In the order created by AUGUSTUS half the army, the legions, was to be recruited among the Roman citizens, the other half, the so-called auxiliary troops, among the provincials, who after their discharge received the citizenship. In this manner many provincials and their descendants became Roman citizens. AUGUSTUS determined that the legions were to be recruited from Italy and the oldest colonies of Roman citizens in the provinces, and the *élite* troops — the praetorians — from certain districts of middle Italy, which had pre-

served the purest Roman blood. This principle, however, could not be maintained. In the first century more and more citizens from the provinces penetrated into the legions, and recruits from all parts of Italy were found among the praetorians. The old recruiting districts became more and more deficient. HADRIAN inverted the principle as to the recruiting of the legions: from his time they were recruited from the districts where they camped, i. e. the borders of the Empire, where civilization, except for what was brought by the army, was at its lowest. SEPTIMIUS SEVERUS dissolved the old Italian body of praetorians and created a new one recruited from the legions. In this manner the army was barbarized and in the third century the way to any leading post was through the army [10]. From the time of MAXIMINUS THRAX the emperors were barbarians, many of them Illyrians; in all probability they belonged to the refractory people that we know in our time as Albanians. They turned the Empire upside-down in the third century, but the vigour of these emperors did at last create order. The lack of recruits, however, was not due entirely to the diminishing number of the civilized population: here the deep-rooted pacificism of the age also made itself felt; but it vigorously contributed to the immixture of barbarians and provincials in the governing classes. From the time of DIOCLETIAN the best bodies of troops were recruited from the Germans within and without the borders of the Empire.

The mixed character of the population of the capital is attested by many ancient authors. We can hardly imagine the extent of the admixture; only Constantinople, the most cosmopolitan city of the world, can give us an idea of it. CICERO calls Rome a city created by the confluence of the nations, four centuries later the emperor CONSTANTIUS wondered at the haste with which all the peoples flowed together to Rome. LUCAN, the poet and friend of NERO, says that Rome was populated not by its own citizens but by the scum of the world. The Oriental element seems to have been very conspicuous. A famous passage in JUVENAL states that the poet cannot like this Graecised Rome, but that the least part of the scum is composed of Greeks: the Syrian Orontes has flowed into the Tiber, with foreign languages and foreign manners.

The Jewish population was considerable. In the year 4 B. C. it is said that 8,000 Jews accompanied a deputation to the Emperor. TIBERIUS turned them out and deported 4,000 to Sardinia, but when CLAUDIUS some years later wished to do the same, they had become

so numerous that the plan could not be carried out. In the eastern provinces the Jews were very numerous, in Egypt they are considered to have amounted to the eighth or seventh part of the population, in Cyrenaica and Cyprus they were killed by hundreds of thousands in the pogroms, in Asia Minor and Southern Italy they were numerous, in Africa, Spain, and Southern France not few. But after the fall of Jerusalem and the great rebellion in the reign of HADRIAN the Jews separated themselves from the rest of the population; hence their importance in the mixture of the races was not so great.

In ancient times the Jews were not merchants and bankers as now. This position was occupied by the Syrians. In the last two centuries B. C. we find many Italian merchants in the East. They were especially bankers and slave- and corn-merchants, and their trade depended on the power of Rome. But when the abuses in the provinces were repressed by the emperors, the Italians disappeared and their places were taken by the provincials. The real merchants were the Syrians, who had important factories in Italy and who appear in every province. They were numerous e. g. in Gaul, where even in the sixth century they were organized into separate Christian churches, at least in Paris and Orleans. SALVIAN mentions the hosts of Syrian merchants who have inundated all the towns and think only of lies and falsehood. The merchants of Italy were not Romans by birth. They were enfranchised slaves, who in this manner had obtained the citizenship [11].

The enfranchisement of slaves is a very important cause of the alteration of the population; it took place on a large scale. It was a point of honour for a noble or wealthy Roman to enfranchise his slaves, at least when he made his will. AUGUSTUS regulated the enfranchisement. The number of slaves which it was permitted to enfranchise was regulated according to the number of slaves which a man possessed, but was in no case permitted to exceed one hundred. The freedmen were in a socially inferior position, but their descendants attained the full citizenship and their grandsons might even become senators. A discussion that took place in the senate in the reign of NERO is very illuminating. It was said that the enfranchised slaves were numerous, they crowded the tribuses and the inferior positions in the state, most of the knights and many of the senators were descendants of freedmen. If the freedmen were turned out, there would be a lack of free citizens.

The freedmen formed a very important part of the population in the earlier centuries of the Empire. It is a burning question whence they originated. A preliminary matter is, which slaves were enfranchised? Those, naturally, who personally attended on their masters and had charge of his business. The slaves of the farms were not valued much more than the beasts of burden and had little better prospect of being enfranchised. For attending on the master and managing his business no mere barbarians were fit; some civilization, such as was found among the able Orientals, was required.

An examination of the statements of the inscriptions concerning the nationalities of the slaves shows that this is true. They corroborate the old saying that the Syrians were a people of born slaves. Most numerous after the Syrians are the Graecised inhabitants of Asia Minor and the Jews. More than half the workers of the Italian potteries have Greek or Oriental names [12], and the names of the artisans of other crafts convey the same impression. Next in numerical importance come the Egyptians and Ethiopians, but in the case of these peoples the external differences were so great that they never became so perilous as the other races mentioned. In Europe no people was predestined to slavery, although some, but not many, slaves originated from European countries. The barbarians of Europe went into the army instead. For instance only two Pannonians are mentioned as slaves, but men of this race crowded into the army [13]. The importation of slaves and the enfranchisement brought in Orientals more especially, and to this fact is largely due the orientalism which is a prominent feature of the later Empire.

There is yet another source for the alteration of the folk-stock, which did not have such an immediate effect as the enfranchisement of slaves but which must in the end have been of considerable importance, viz. the transplantation of whole tribes from beyond the northern frontiers into the Empire. Augustus' general, Agrippa, had already transplanted the German Ubii from the right to the left bank of the Rhine. Some years later 40,000 Sugambrians and Swebians were settled in Gaul, and 50,000 Dacians were brought from the districts north of the Danube into Thracia. In the reign of Nero great hosts with chiefs, wives, and children — it is said to the number of 100,000 — were brought over the frontier from the same districts. When Marcus Aurelius had conquered the Marcomannians and the Quades he settled those peoples in great masses in the Empire — in Dacia, Pannonia, Mysia, the Roman Germany, and even in Italy.

These settlers did not attain to the citizenship; they became something like serfs and in a later age contributed considerably to the army.

Professor SEECK contends that this invasion of Germans caused an important change [14]. The western part of the Empire was Germanised and the birth-rate commenced to increase, he says. In the wars of the third century there is never any mention of a deficiency of recruits, as in former times. He refers to the description of the Gauls by AMMIANUS MARCELLINUS in the fourth century to show that they were Germanised; they were well able to fight, had blue eyes, fair hair and complexion, and were of high stature. But our ideas of the Celts are contrary to the ancient testimonies [15]. As long as the government desired to recruit the army from the civilized population, there was a lack of recruits; that the recruiting should be difficult in the great wars of MARCUS AURELIUS is comprehensible, since pestilence ravaged the Empire. As soon as the emperors determined to recruit the army from the provincials (Pannonians, Illyrians, Africans etc.) there was no lack of recruits. In older times a very small minimum height is given for the recruits, 1,48 m.; in 367 A. D. on the contrary a very high one, 1,63 m., and this is believed to demonstrate a change in the supply of recruits. But the former figure refers to voluntary recruits, of which there was no surplus in these times, the latter to such recruits as landed proprietors had to deliver from their serfs. They were no less anxious to furnish as bad men as possible than the government to get the best men. There is no evidence for a swift change of blood, but the importance of the Germans that were transplanted into the Empire is not to be underestimated. They formed a strong addition to the barbarian population and paved the way for the German occupation at the end of the Empire.

What has been set forth as to this point may convey the impression that an inverted selection took place, and in reality there was something like it. The peoples that had created the ancient culture and the Roman Empire diminished in number, and the gaps were filled up by provincials. This process led to a sinking of the culture, in proportion as the less civilized provincials ousted the old citizens, and lessened the coherence of the Empire, which depended on the people that had created it. But this problem we have not to consider here. The process concerns us directly in so far as the old races were ousted by races of lesser value. This fact may have been of importance, but in view of their later history it is risky to contend that the Semites and the Germans were less able races, and

from these two peoples came the main streams which changed the stock of the population.

The crucial problem is another and is one that is contained within the Empire itself to a far greater extent than may have appeared up to this point. The Roman Empire was a motley of different peoples, races, and languages. This fact has been somewhat obscured because in the West the old languages were ousted by the Latin and died without leaving traces (except the Basque). But this is a superficial matter. The races themselves persisted and took part in the mixing of the peoples, although they changed their languages. It is of the first importance to form a concrete idea of how manifold and deep and great the differences were [16].

At the commencement of the Empire the population of Italy seemed to be rather homogeneously Roman. It had been Romanised during the last centuries of the Republic, but the old races had not died out, they added their contribution to the population. The Oscan-Umbrian tribes were very closely akin to the Romans and they spoke dialects of the same language, but there were once many other peoples in Italy of different races, in the north Celts, in the north-east and south-east Illyrian tribes, in the south Greeks, besides many native tribes, Oenotrians, Sicanians, Siculians, etc., about whose race we know nothing. The Etruscans played an important part but they are yet an unsolved riddle. The art shows that they had a very marked and peculiar physical type. We can read their language but cannot understand it, all attempts to connect it with any other language having failed; the language died out at the commencement of the Empire. In N. W. Italy and S. E. Gaul we find the great people of the Ligurians, which up to the imperial age preserved in some parts its liberty and its very primitive mode of living. The Ligurian language is lost, the connexions of this people with other races, if it had any, are unknown [17]. The most probable view is that the Ligurians were the original inhabitants of these districts, and were supplanted by the Celts who invaded the Po valley about 400 B. C. Certain students have tried to show that the type of the people and the language of the once Ligurian districts preserve some peculiarities which are supposed to be the last traces of this extinguished race.

Gaul, i. e. France and the Po valley, was so called after the ruling race, the Gauls, who are also called Celts. During ancient times Celtic was the common language of the inhabitants and was spoken even by the noble families. IRENAEUS had to preach in Celtic in

Lyons, about 200 A. D.; it was permitted to use Celtic in writing wills. The language survived at least into the fifth century. The Gauls had to learn Latin with toil and labour.

In France too the Celts were conquering immigrants, who had settled more especially north of the central mountainous region. In the south-eastern parts lived the Ligurians, in the south-western the Iberians. This is another non-Aryan people whose riddle is unsolved, but it seems as though the Iberians were the original inhabitants of these parts of France and Spain. Small Celtic hosts had penetrated into Spain, mixed up with the Iberians, and formed the Celtiberian tribes. In north-western Spain there still survives the Basque language, the only remnant of the pre-Aryan languages of Europe. Its grammatical structure and vocabulary differ totally from those of other languages. It is tempting to connect it with the Iberian language, but the Iberian inscriptions, although not interpreted, do not seem to corroborate this supposition. Hence some students have referred the Basques to the Ligurians, who perhaps also inhabited parts of Spain, others have tried to connect Basque with the Berber language, but the Ligurians are, as to the language, an unknown quantity and the connexion with the Berbers is not warranted by evident facts.

In the British Isles the Celts are immigrants. Consequently we may expect to find here considerable remnants of the older aboriginal inhabitants. Such were e. g. the wild Picts of Scotland, whom the Romans never subjugated. There is a great difference between the two peoples that still speak Celtic languages — the Irish, who often have fair complexions, and the usually small and swarthy Welsh. The supposition at once arises that the Welsh are Celts in language only, and not in race. This theory has been advanced by English scholars, who have tried to find further connexions, e. g. with the Iberians and the native races of North Africa, but without any very certain evidence [18]. The theory is of course opposed to the common idea that the Celts were a swarthy people of small stature, but this is an inference from the modern Frenchman, who is held to be the real descendant of the ancient Celts. It conflicts with all testimonies of ancient literature and art. If we desire to know the physical type of the ancient Celts we must needs follow these indications, and they show unanimously that the Celtic type was much more akin to the Teutonic — blue eyes, fair complexion and hair, high stature, and a ferocious mind. If facts are to speak it must be admitted that the Celtic type in France generally was merged in the original inhabitants, and this is only

natural. It is the usual fate of an invading, conquering people, even if they are able to impose their language on the conquered.

Celtic tribes had also penetrated into Pannonia and the Balkan peninsula, but were too few to acquire very much importance. The inhabitants of Pannonia seem to have been chiefly Illyrians. In Dacia and the eastern Balkan peninsula lived the Getans or Dacians, who belonged to the Aryan race, although they never had any considerable historical importance. Our information here is more than usually scanty and does not admit of any suppositions as to the older inhabitants who may have lived in these countries.

The remaining province of the western part, Africa, is better known. The Punic language survived during the imperial age. Most of the hearers of St. AUGUSTINE understood Punic: it was spoken by the peasants. The church had its difficulties with their language; no one was readily made a bishop who did not know Punic. In the interior lived the Berber tribes, who still retain their peculiar language and racial type.

In the East the position is simple and clear, except in the case of Asia Minor. In Egypt and the Semitic Orient the Greek culture and language had never been more than a thin varnish that was soon worn off. The ethnology of Asia Minor was extremely mixed. No land had been exposed to invaders to such a degree as this [19]. The Empire of the Hittites had been crushed in the twelfth century B. C. by invading Aryan tribes, the Phrygians, but the race survived. It is supposed that it was merged into the Armenians and perhaps partly into the Jews. Lydians, Carians, and Lycians have left inscriptions. An attempt has been made to connect the language of the last-named with the Aryan languages, but with doubtful success. The Lydian language seems to be distinct from others [20]. Later on other Aryan tribes had invaded the land, Thracians in the commencement of the first millennium B. C., and Celts in the middle of the third century B. C. The interior of the country was called Galatia after them. The Hellenising was wide-spread, but in spite of this the old languages survived more vigorously than is generally surmised, and this is also an evidence for the subsisting of the old races. The Mysians, who seem to have been a mixture of Thracians and Lydians, still spoke their own language in the beginning of the fifth century A. D. So also did the famous Isaurian robber tribes at the end of the sixth. The same was the case in Lycaonia; the Phrygian language survived at least into the fifth century [21]. The surface seems to be

Greek, but underneath great racial differences survived, which found an expression in the Christian sects of Asia Minor; their stronghold was the native population of the country.

Our information is scanty and the research is difficult, but the broad outlines which have been sketched above will be sufficient to convey a concrete idea not only of how many races, peoples, and languages were contained in the Roman Empire, but also of how radically different most of them were [22]. Modern Europe is apt to give an erroneous impression. Except for a few unimportant peoples of other races (Finns, Hungarians, Turks and a few others) it seems to present the image of an Aryan population that is separated into different peoples but has sprung from the same source. This is true only as to the languages. The kindred languages cover great racial differences, although new races have developed from the ancient blend of races. The very vivid discussion on the origin and splitting up of the Aryan tongue has obscured the comprehension of the older racial status of Europe. The leading idea is (at least unconsciously) that of an ancient original unity that was differentiated and split up. In the case of the original inhabitants of Europe we must instead of a unity imagine a multiplicity of different races and languages; the latter were ousted by the language of the invading Aryan tribes and died, the races were seemingly merged in their conquerors. The victorious spreading of the Aryan languages put an end to the multiplicity of earlier languages — e. g. Etruscan, Ligurian, Iberian, etc. — and introduced Aryan languages that were kindred with one another. This process was strongly advanced during the Empire; S. W. Europe, which up to this time had spoken non-Aryan tongues, was assimilated. But the enigmatical Basque language still survives as a reminder of what has once been.

It is in this light that the racial problem of the Roman Empire is to be viewed. As long as the peoples of western Europe lived in their old primitive and independent condition the status was rather stable. The Greek colonists were few and the peoples on whose shores they had founded their towns were often openly hostile to them. In Italy the Latin and Oscan-Umbrian tribes pushed out the original inhabitants more and more. The connexions with Greece and the Orient were few. The invading Celtic tribes brought disturbance, but these tribes settled in certain districts. In S. W. France and most of Spain the old races were not disturbed. The invasion must

however have involved a certain mixing up of the races, and this is testified by the name of the Celtiberians. But the culture was little developed, the intercourse was rare, the intruders were not able to absorb the old races, they consolidated themselves within somewhat narrower frontiers. The tribes were independent and hostile to each other. This would have prevented a mixing up of the races on a larger scale, even if the conditions for such a mixing up had existed at all.

Such were the conditions introduced by the Roman Empire. The peace of the Roman emperor, imposed by the Roman government, wiped out the old frontiers. The different tribes were subjected to the same administration and the same culture was opened to them all. The excellent Roman roads favoured the intercourse, while culture, trade, and the needs of the Empire increased it. The mixing up of the different races and peoples of the Empire was begun and increased by all the causes which make the inhabitants of a civilized state move from one part of it to another. What some of these causes were we have shown in the foregoing pages. The men who in former times had lived and died and propagated their kind within the frontiers of their own people were mixed up, as it were, in a great bowl as wide as the limits of the Empire, and peoples from beyond the frontiers were thrown into the same vessel. This is the fundamental fact the importance and consequences of which we have to consider.

It may be said that the problem was whether the less civilized peoples should be merged in the civilized — the Romans and the Greeks, to whom the culture and coherence of the Empire were due — or whether the civilized were to be absorbed by the less civilized. As we have seen, the circumstances were not favourable. The effects upon civilization were very important: the bankruptcy of the civilization and sinking of the general level of culture in the hardships and wars of the bad third century destroyed much more than all the cruelties of the emperors. But it is not our task here to investigate this point. The mixing up of the races involves not only a problem for civilization but also a biological problem, and to this we must now return. I think it may be understood in the new light of recent researches on genetics.

The species man is extremely variable, being surpassed in this respect by only a very few other species. Each race is the product of a historical development, although the history of its development belongs to a time past long ago, which has never been recorded. The

condition for the developing of a race is that a group of men, who may be counted in hundreds or in millions, shall live for a considerable time in at least relative isolation, so that foreign disturbing elements are kept out. If it be supposed that this group originally contained a motley mixture of internal and external dispositions, the natural conditions under the sway of which the group lives will be favourable for some of these dispositions and unfavourable for others. The natural conditions have the same effect as the conscious interference of a breeder trying to produce a certain race of some species of animals, although more slowly and not to the same extent. The effect will be stronger in proportion to the smallness of the group and the intensity of inbreeding. The outcome of this selection depends much more on the dispositions which originally existed and which in the development of the race attain to ascendency than on the external *milieu*. Why some races are excellently adapted to the natural conditions of life of their country and are yet unable to achieve a higher political and intellectual development, and why on the other hand other races are able to create a culture and a political organization is a riddle which is concealed in the darkest riddle of all, the human mind, the variability of intelligence and volition, for these too are properties which vary with the race. It is only that we cannot grasp them definitely.

Primitive conditions are favourable to this breeding of races. The population is thin and split up into small groups. Intercourse is rare. The tribes are hostile or at least foreign to each other and occupy each a definite district. A fact of profound importance for the development of society and races is the claim to possess the district in which the tribe lives; this seems to be founded in the nature of man, as well of some species of animals. Foreigners who penetrate into the district of the tribe will be expelled or killed. The tribe maintains its purity from foreign elements until the advance of culture introduces slavery, which is first applied to the women. In primitive conditions this occasion of the mixing of the races is of no great extent or importance. Neighbouring tribes are often kindred.

Under primitive conditions we have consequently to expect a multiplicity of characteristically different races, although the differing capacity of different races to maintain themselves in the struggle for life and the combats against other races causes a certain race to spread itself over a wider territory, while the migrations which originate in over-population and an innate desire to wander introduce a foreign

race into a country. If we take these two circumstances into account, we have the status of Europe and Africa before the Roman conquest. In Africa we find Berbers and the immigrant Punics, in western Europe Iberians, Ligurians, the immigrant Celts, and plenty of other races of whom we have no sufficient knowledge. The ethnology of Italy seems to be more varied; our information is here richer. Apart from the old inhabitants and the immigrant Aryans there were the enigmatical Etruscans, who cannot be connected with any other people. The Balkan peninsula and the countries south of the Danube were inhabited by Aryans and perhaps by remnants of an older population. Asia Minor was from very ancient times a melting-pot for many different races. Syria was inhabited by Semitic tribes which the policy of the Assyrians had transplanted and mixed up. In Egypt the old stable race preserved itself, but the mixing up with the foreign masters of the land and immigrants here also caused a mingling of races which may possibly have been an important factor in the trouble and decline at the end of antiquity.

When under the shelter of Roman peace and Roman administration all these races — those mentioned are only the most important of the races known — were mingled with each other, the result was an unlimited bastardizing. Bastardizing conveys perils which cosmopolitanism did not acknowledge but which modern science has shown to be real. The race is a group of men with definite hereditary dispositions which through the above described natural selection have become to a certain degree firm and fixed. There are races of more and lesser value. Bastardizing between two races which differ from each other to more than a certain degree results in the deterioration of the race, at least viewed from the standpoint of the better of the two. The aversion to mixed marriages, e. g. to marriages between Europeans and negroes, is consequently just from a genetic point of view. The danger is yet more insidious if the races are on the one hand so different that the bastardizing involves the peril of a deterioration of the race, but on the other hand do not differ so much in externals that the aversion to mixed marriages makes itself felt. This aversion is however a very feeble defence against the mixing up of races, and its strength depends on the mind of the age.

The crossing of races, through which a better race is superseded by a worse, is however neither the only peril nor the greatest. A race that is at least to a certain degree pure is physically and psychically a fixed type, which precisely through the firmness and fixedness

of its dispositions is able to create something to which its dispositions predispose it. If these dispositions are of such a kind as to enable the race to achieve a higher culture or to organize a state, as was the case among the Greeks and Romans, the result will be a certain form of culture and of state, moulded according to fixed laws and customs of life. The result of the bastardizing will be a motley blend of the different hereditary dispositions of the races which are crossed. Mere chance brings different dispositions of different races together in almost infinitely varying fashions. But this does not suffice. Dispositions which were formerly concealed, lying latent in one or the other of the crossed races, will appear on the surface and make the product of the crossing yet more motley and incalculable. The unity and harmony of the race and the individual will be destroyed, the personality loses its balance. The individuals which are born out of this crossing fail to achieve a firm and fixed type. Psychically they lack a definite direction and vacillate indecisively between conflicting and unconnected hereditary dispositions. They may often possess great intelligence, but the moral strength is wanting. This state of affairs is due to biological factors but gets still worse if — as was the case in the Roman Empire — the fixed form of the mental life at the same time breaks down and is transformed.

Bastard races have a bad reputation. If Levantines, Eurasians, Mestizes etc. are mentioned everyone feels how deep-rooted is the objection against them. People are wont to say that this bad reputation and the moral weakness of the bastards are due to the unfavourable conditions in which they are born and bred, usually as illegitimate and neglected children, disowned by the kinsfolk of both father and mother. But this is not the full explanation, it is only superficial; at the root lies the destroying effect of the bastardizing on the personality. The Roman Empire became more and more filled by bastards. The bastardizing was strongest in the ruling country, Italy, whither people from all the borders of the Empire flowed together, and was stronger in the upper civilized classes than in the lower, which did not move about with the same frequency [23]. But the army, the trade, and the general intercourse carried the bastardizing into every corner of the Empire. The swiftness of the process is not to be wondered at. Contrary to the slow development of a race, the bastardizing shows its effects even in the first generation, but is of course increased by the crossing of the bastards. Whether it is to set its stamp on the people will depend solely on the extent

of the process, and it has been shown that in the Roman Empire it was carried out on the largest scale.

A bastardizing to this extent results in the mingling of better and worse races into a motley and indefinite mass without firm mental or moral characteristics. This is a sufficient explanation of the decline and fall of the ancient culture and the Roman Empire. But even if the bastardizing and mixing up of the races leads by its immediate effects to chaos, this is not the ultimate result. New races may emerge from the chaos and be able to reconstruct that which was destroyed. We know the conditions for such a development. They are that the bastardizing shall cease and the people shall be isolated so that the mixture gets its chance and has time to become settled and purified. In this way are given the conditions for developing a new race from the motley blend, the nature of which depends on the circumstances.

The above-mentioned conditions were realised at the commencement of ancient history. The ancient culture peoples, the Greeks and the Romans, invaded their countries from without and settled themselves among peoples of foreign races. The Greeks and the Romans of history are a product of a blending of races. Our knowledge of the Romans is very scanty. If the oldest population of Rome was a blend of Latins and Sabines, that does not matter much, because these tribes were already very closely akin. But it is certain that the Etruscans held sway over Rome some time towards the end of the period of the kings, and their culture exercised a profound influence on the city. They lived next-door, on the other bank of the Tiber, and it may be supposed with certainty that the Romans had a considerable admixture of Etruscan blood.

Greece is better known than Italy and her history enables us to follow the process more closely. Recent discoveries have revealed to us the wonderfully high culture of the early and middle second millennium B. C., which is known as the Minoan and Mycenaean culture. It is certain that the people which created this culture was not Aryan: it was perhaps akin to some peoples of Asia Minor, though others maintain that its kinsfolk are to be found in northern Egypt. The invading Aryan tribes, the Greeks, settled among the original inhabitants of Greece in the same second millennium and at last destroyed the old culture. The centuries between the decay of the Mycenaean culture and the commencement of the historical age are a blank. We know only that the culture was utterly debased. The small di-

stricts of Greece were isolated from each other. This is shown by the geometrical style of vase-painting which belongs to the ninth and eighth centuries B. C. The Mycenaean style of vase-painting is the same wherever Mycenaean vases are found, in or outside of Greece. The geometrical style, on the contrary, has very characteristic differences: it is quite easy to say in which island or province a vase or even a sherd has been made. The ancient towns were small, the district was very limited, and the inhabitants were not very numerous. Each of these towns was wholly independent and sovereign, composing a state with its own rights. The bitterest enemy was usually the neighbour. In this narrow frame the people lived and — married. Consequently inbreeding was the rule and was strongly accentuated by the smallness of the population. In Athens at a somewhat later age the law enforced it; nobody could become a citizen if both his parents were not citizens of the town. This isolation and inbreeding created the race to which ancient culture and the foundations of our own culture are due. Italy, which at last conquered the world and organized the Empire, underwent much the same process.

The process was repeated, but on a larger scale, after the decay of the ancient culture and the fall of the Roman Empire and the settling down of the foreign conquerors in its provinces. Letters and education, as far as they survived at all, were limited to very few. The decay of the material civilization changed and fettered the lives even of the poorest classes. We may compare the ages e. g. of HADRIAN and of the Merovingians in order to perceive this. Intercourse ceased. The old Roman roads, on which the peoples of the Empire had penetrated into all parts of it, fell into disuse, were broken up, treated as quarries, or became overgrown by herbs and woods. Society was split up into small independent and self-supporting unities, — this is the feudal system — the inhabitants were rooted fast in the soil. So there reappeared the primitive conditions under which every man takes his wife at his own doors. In this isolation of the small groups new races and new peoples developed out of the mixed human chaos of the Empire during the Middle Ages. These are the peoples of modern Europe, and the outcome of their racial instincts is seen in the national states of modern Europe, whose frontiers form to some degree an effective barrier against a race-blending of such a destructive character as that which was the most active cause of the decay of ancient culture and the fall of the Roman Empire. The Nemesis of history has caused the consequences of victory to be

fatal to the victors, who have been merged and lost in the broad masses of the conquered races.

NOTES.

[1] O. SEECK, *Geschichte des Unterganges der antiken Welt*, I, the chapter »Die Ausrottung der Besten».

[2] K. J. BELOCH, *Die Bevölkerung der griechisch-römischen Welt.*

[3] K. J. BELOCH, *Griechische Geschichte*, I: 1^2, p. 66.

[4] MARTIN P:N NILSSON, *Den romerska kejsartiden*, II, ch. 4.

[5] J. ILBERG, *Zur gynäkologischen Ethik der Griechen*, Archiv für Religionswissenschaft XIII (1910) 1 sqq.

[6] L. FRIEDLÄNDER, *Darstellungen aus der Sittengeschichte Roms*, I^8, pp. 419 sqq.

[7] The *lex Julia de maritandis ordinibus* and the *lex Papia Poppaea.*

[8] For references see e. g. the article Alimenta in PAULY-WISSOWA, *Realencyklopädie der klassischen Altertumswissenschaft.*

[9] M. GELZER, *Die Nobilität der Kaiserzeit*, Hermes L (1915) 395 sqq.

[10] A. v. DOMASZEWSKI, *Die Rangordnung des römischen Heeres*, Bonner Jahrbücher 117 (1918). — H. DESSAU, *Die Herkunft der Offiziere und Beamten des römischen Kaiserreiches*, Hermes XLV (1910) 1 sqq.

[11] V. PARVAN, *Die Nationalität der Kaufleute im römischen Kaiserreich*, Dissertation, Breslau, 1909.

[12] H. GUMMERUS, *Romerska krukmakarstämplar*, Eranos XVI (1916) 176.

[13] M. BANG, *Die Herkunft der römischen Sklaven*, Rheinisches Museum XXV (1910) 225 sqq.; *Nachtrag*, ibid. XXVII (1912) 189 sqq.

[14] SEECK, *loc. cit.* pp. 385 sqq.

[15] See, p. 380.

[16] The old standard work is H. D'ARBOIS DE JUBAINVILLE, *Les premiers habitants de l'Europe*^{2} (1889). For a more recent review see H. HIRTH, *Die Indogermanen* I pp. 34 sqq.

[17] Some authors, following D'ARBOIS DE JUBAINVILLE, take the view that the Ligurians were an Aryan people, but the evidence adduced is exceedingly slight.

[18] See e. g. J. BEDDOE, *The Races of Britain.*

[19] See my paper *Den stora folkvandringen i det andra årtusendet f. Kr.* in Ymer 1912, pp. 455 sqq. On the languages of Asia Minor P. KRETSCHMER, *Einleitung in die Geschichte der griechischen Sprache*, pp. 289 sqq

[20] *Sardis*, Publications of the American Society for the Excavation of Sardis, vol. VI, *Lydian Inscriptions*, by ENNO LITTMANN.

[21] K. HOLL, *Das Fortleben der Volkssprachen in Kleinasien in nachchristlicher Zeit*, Hermes XLII (1908) 240 sqq.

[22] The anthropological school of Professor SERGI, RIPLEY and others has tried to show that there existed in Europe from very old times three races: the fair, dolichocephalic Northern race, the dark-haired, grey-eyed, and brachycephalic Alpine race, the dark-haired, dolichocephalic Mediterranean race, and that, in spite of all invasions and crossings, these races still maintain themselves in their respective districts. I cannot discuss this theory here, it would also imply a

discussion of the question as to what is to be understood by »race». (For my views as to this point see my above-cited paper in Ymer 1912, pp. 465 sqq). There are races with varying degrees of racial differences. I wish only to point out that the above-mentioned theory may not be inconsistent with the view that is advanced here. The signs by which these three races are recognized are purely physical. Here it is in the first place a question of psychical differences. It may be that the physical properties have persisted on the whole but that the psychical ones have changed in the formation of the new races which have developed from the blending of the races in Europe.

[23] Cp. the dates given above (pp. 384 sqq.) for the provincial origin of emperors and senators.

THE LOCATION OF A NEW SECOND CHROMOSOME EYE COLOUR GENE IN DROSOPHILA MELANOGASTER

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IN a back-cross of a single female, heterozygous for the sex-linked recessive genes eosin (eye colour), vermilion (eye colour) and forked (bristles) to eosin vermilion forked males, there occurred (Oct. 15, 1919) out of a total of 120 flies 2 females and 4 males having a light brownish eye colour, which seemed to differ from all the eye colours expected in this test. These flies were inbred, and for some generations selection was carried out in order to get rid of the sex-linked genes present, and a stock was obtained which bred true for the brownish eye colour mentioned.

On the assumption that this character, called brown (*bw*), was due to a new mutation, an experiment was carried out in order to determine the chromosome to which its gene belonged. Brown females were crossed to males heterozygous for the dominant characters Star (*S*) in the second chromosome (at 0,0) and Dichaete (*D*) in the third chromosome (at 38,5). Both the males and the females obtained in this cross had wild type red eyes, which proved that the gene in question was recessive and not sex-linked.

Star Dichaete females from this mating were back-crossed singly to brown males (BRIDGES and MORGAN, 1919, p. 246: the double dominant test) with the following result:

S D	*S*	*bw D*	*bw*	*S bw D*	*S bw*	*D*	+
261	264	246	308	93	106	126	138

This proved that there was free assortment of Dichaete and brown, but seemed to show a coupling to Star, corresponding to an amount of 30,0 per cent of crossing over.

This result would indicate that the locus of brown was in the second chromosome about 30 units from Star, and brown flies were now made homozygous (concerning the best method of making up a

triple recessive stock see BRIDGES, 1919) for the two second chromosome recessives dachs (legs, *d*, at 29,0) and black (body colour, *bl*, at 46,5) in order to determine the linkage relation of brown to these two previously known loci. In a total of 2578 flies there was found a crossing-over percentage of 45,7 between brown and black and 46,7 between brown and dachs.

This result raised doubts as to the correctness of the classification in the Star Dichaete back-cross, as there was a discrepancy between the linkage values obtained in the two tests. A brown black male back-cross, i. e. homozygous brown black female × heterozygous male, was accordingly carried out. Since there is no crossing-over in the male, this cross would show conclusively whether or not the gene was located in the second chromosome. The result was:

bw bl	+	*bl*	*bw*
70	53	0	0

which proved that the locus of brown was in the second chromosome.

The black brown linkage value obtained above (45,7 %), seen in connection with the values obtained in the Star Dichaete female back-cross, made it appear likely that the locus of brown was at the right end of the second chromosome, and in a final experiment it was decided to determine the linkage relation of brown to genes which had their loci in this part of the chromosome. As such were used plexus (venation, *px*, at 98,3) and arc (wing, *a*, at 97,5).

TABLE 1.

Repulsion test. P_1 mating, plexus ♀ × brown ♂; B. C., F_1 wild type ♀ × plexus brown ♂.

Nov. 27. 1920	non-cross-overs		cross-overs	
	px	*bw*	+ *px*	*bw*
280	122	149	4	6
281	103	113	5	4
282	98	97	3	2
283	95	110	4	4
286	72	101	4	7
287	56	71	3	0
325	29	23	2	0
Total	575	664	25	23

TABLE 2.

Coupling test. P_1 mating, plexus brown ♀ × wild type ♂; B. C., F_1 wild type ♀ × plexus brown ♂.

Jan. 25. 1921	non-cross-overs		cross-overs	
	+	*px bw*	*px*	*bw*
322	17	12	2	1
323	56	38	1	1
324	12	11	0	1
326	21	28	1	1
327	10	13	0	1
328	29	22	0	1
329	16	17	1	0
Total	161	141	5	6

TABLE 3.

Triple recessive test. P_1 mating, arc plexus brown ♀ × wild type ♂; B. C., F_1 wild type ♀ × arc plexus brown ♂.

Feb. 8. 1921	0			1			2		
	+	*a px bw*		*a*	*px bw*		*a px*		*bw*
334	73	83		1	1		1		5
335	82	63		1	1		5		3
336	82	82		1	0		6		7
337	106	73		1	4		1		7
338	79	83		0	2		4		2
339	87	104		0	2		2		0
340	94	75		2	2		3		3
Total	603	563		6	12		22		27

As seen from tables 1—3, 108 cross-overs between plexus and brown were obtained in a total of 2,833 flies. This means that there is a distance of 3,8 units between the two genes mentioned. In the arc plexus brown test no flies were obtained which were arc brown or plexus. The locus of plexus is accordingly between the loci of the two others. Since arc and plexus according to the most recent data are mapped as having their loci at 97,5 and 98,3 respectively, the locus of brown is found to be at 102,1.

The eye colour of newly hatched brown individuals is a pure, transparent brown, lighter than the wild type red. This colour rapidly

deepens and at the same time changes into a ruby tone, strikingly like the one found in young purple flies. The colour retains its transparency also in old flies. When we consider the degree of dilution in young brown flies, it seems surprising that the eosin eye colour does not show a marked dilution when combined with brown. Likewise brown was tried in combination with the earlier second chromosome eye colour purple, but failed to show a conspicuous dilution in double recessive purple brown flies. In fact, these double recessive flies cannot be distinguished from pure purple flies.

The brown flies are of good viability and of normal fertility. They may be distinguished with perfect accuracy and ease from wild type individuals.

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SPONTANEOUS CROSSING IN THE GARDEN BEAN, PHASEOLUS VULGARIS

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SPONTANEOUS crossings are by no means rare in common garden beans, which every one knows, who has worked on the improvement of this species or used it for theoretical investigations.

The estimates of the approximate percentage of the spontaneous crossing are, however, rather different. Some Swedish plant-breeders are of the opinion that it is probably quite inconsiderable, while others assume it to average up to 5 %. Even in the literature the statements are rather at variance. Thus DARWIN considers it sometimes to be very great. FOCKE holds that it some years is very important, v. TSCHERMAK asserts that spontaneous hybrids now and then are found (FRUWIRTH 1910). EMERSON (1916) has calculated the number of spontaneous hybrids found in his cultures; it varied between 0 and 10 per cent. No attempts seem to have been made to ascertain the percentage by way of experiments.

In my investigation I have made use of the following method. Small plots of the variety to be tested as to its tendency of cross-pollination were sown in the large field cultures of beans. These plots are here called »isolations». These were located at a distance of about 20 metres from each other, and each plot contained only 5 or 6 beans. The field cultures of the bean were always put in rows, and the seeds of the isolations were sown in the rows (not between). As they were put in the soil at the same time as the rest of the cultures the development of both sorts took place simultaneously. The time of flowering was also the same, a fact of great importance, of course.

Thus every plant of the variety tested was quite surrounded by flowering plants of the large seed culture. As the number of the individuals in every plot was small, most of the crossings which resulted in the isolations must have taken place between plants of the isolation and the field culture beans, and only very few between plants belonging to the isolated variety. The percentage of spontaneous crossing should accordingly come very close to the maximal one.

In beans it is impossible to determine by mere inspection of the seed whether crossing has taken place or not; it is at once seen, however, when the F_1-plant and its seeds are at hand. Thus it is necessary to grow another generation of the isolated plants.

The experiments to be dealt with in this paper were begun in 1918. Not less than 18 varieties in 162 isolations were tried that year. Unfortunately the labels of two-thirds of these isolations were destroyed during the cultivation of the field culture beans and could not be found again. The seeds of the remaining isolation were sown in the experimental field the following year, care being taken that the seeds from each plant were sown separately. Some of the lines did not germinate, and therefore only 44 remained to the definitive calculation.

As experiments from only one year must be considered insufficient I deemed it necessary to repeat the experiments in 1919. The number of varieties was reduced to 8, and these were sown in 123 isolations in all. A great number of isolations were also destroyed this year, therefore only seeds from 86 plants could be sown the next year.

The varieties used are classified as defined in the »Nordiska Jordbruksforskares Förening», viz. in shell-, sword-, break-, asparagus-, and wax-beans. The break- and asparagus-beans, however, have been brought together in one group: haricots vert. The varieties are put in the following main groups:

Shell-beans	*Sword-beans*	*Haricots vert*	*Wax-beans*
Brown bean	Broad sword	Amerikansk repfri	Wax flageolet
Chocolate brown	Dutch sword	Chevrier	
Mottled brown	Kaiser Wilhelm	100 to 1	
	North star	Saxonia	
	Risbrinken	Emperor of Russia	
	Uppland		

Tables 1 and 2 give a comparison of the results obtained in the experiments. Col. 4 denotes the totals of the plants harvested from all the isolations of each variety, and col. 5 the number of plants received from the isolations when their seeds were sown in the experimental field the following year. Table 3 shows the percentage of the crossings received from the main groups of beans.

The percentage of hybrids was, as it appears from the tables, rather the same each year, and amounts to an average of 1,05 %. The

TABLE 1. *Percentage of crossings found in the experiments of 1918—1919.*

1	2	3	4	5	6	7
Tested variety	Bean-culture	Number of isolations 1918	Number of plants 1918	Number of plants 1919	Number of hybrids	% Hybrids
Kaiser Wilhelm.....	Wax flageolet.....	4	12	61	0	0,00
»	Chevrier	1	1	11	0	0,00
Risbrinken	Wax flageolet.....	1	2	2	0	0,00
Dutch sword	»	4	28	239	0	0,00
Uppland sword... ..	»	3	9	19	0	0,00
North star	»	3	3	3	0	0,00
Broad sword	»	2	7	39	1	2,56
Mottled brown	»	4	13	74	1	1,35
Chocolate brown ...	Risbrinken	5	7	39	3	7,69
» ...	Wax flageolet	3	10	40	2	5,00
Brown bean.....	Chocolate brown ...	3	16	261	0	0,00
»	Wax flageolet.....	2	7	48	0	0,00
»	Chevrier	1	2	25	0	0,00
»	Risbrinken	3	11	55	0	0,00
Amer. repfri	»	1	1	3	0	0,00
Emperor of Russia	»	2	5	13	0	0,00
Chevrier	»	1	1	16	1	6,25
»	Wax flageolet.....	1	2	11	0	0,00
	Total	44	137	959	8	0,83

differences between the main groups are, however, rather important. The shell-beans show a percentage of cross-pollination that is considerable higher than that of the haricots vert. The sword-beans are fairly intermediate. The high value found in the haricots vert in 1918 points in quite a wrong direction as only 43 plants of this group were grown this year, giving one hybrid. In fact, it is the only one of this main group found in these experiments, whereas in another trial with a haricot vert, viz. the Steninge Hybrid, 11 hybrid plants were found among 547 recessive steel-coloured, whose parents had grown side by side with the dominant black ones without being isolated. This shows a cross-pollination of about 2 %.

This greater tendency of autogamy in the haricots vert depends probably to some extent on the fact that they begin to flower a little later than the large field cultures (this is at least the case with some varieties). However, this may only be of rather small importance as the flowering period of beans is of relatively long duration.

TABLE 2. *Percentage of crossings found in the experiments of 1919—1920.*

1	2	3	4	5	6	7
Tested variety	Bean-culture	Number of isolations 1919	Number of plants 1919	Number of plants 1920	Number of hybrids	% Hybrids
Chocolate brown ...	Saxonia	7	17	209	3	1,44
» ...	Risbrinken	6	12	152	3	1,97
» ...	North star	3	9	77	10	12,99
Brown bean.....	Saxonia	4	17	352	1	0,28
»	Risbrinken	6	17	286	3	1,05
»	North star	5	17	218	0	0,00
100 to 1.....	»	5	11	137	0	0,00
»	Risbrinken	13	23	252	0	0,00
Saxonia	Chocolate brown ...	1	1	18	0	0,00
»	Brown bean	1	2	7	0	0,00
»	Risbrinken	2	2	10	0	0,00
»	Uppland	2	2	4	0	0,00
»	North star	2	3	18	0	0,00
Amerik. repfri.....	Risbrinken	4	5	35	0	0,00
»	North star	3	4	16	0	0,00
Risbrinken	Chocolate brown ...	1	1	1	0	0,00
»	Brown bean	1	1	23	0	0,00
»	Amerik. repfri	1	1	3	0	0,00
»	100 to 1.....	8	12	162	2	1,23
North star	»	4	8	40	0	0,00
»	Amerik. repfri	2	2	42	2	4,76
»	Brown bean	1	3	55	0	0,00
»	Chocolate brown ...	4	7	53	1	1,89
	Total	86	177	2,170	25	1,15

TABLE 3. *Percentage of crossings found in the main groups.*

Main groups	Shell-beans	Sword-beans	Haricots vert
% of hybrids in 1918.....	1,11	0,27	2,33
% of hybrids in 1919.....	1,55	1,32	0,00
Average	1,42	0,80	0,19

Indeed, one is inclined beforehand to suspect differences in the tendency to cross-pollination, as there are differences in the construction of the flowers with regard to the longer pushing out of the stigma of some varieties than of others.

Of all investigated varieties the chocolate brown beans have given the greatest percentage of hybrids, and this has been the case also in 1918 and 1919; it is not very probable that the result is a mere chance. The greatest percentage of crossings ever found in any isolation was in such a chocolate brown bean. There were in this case 5 plants with a progeny of 34 individuals in all, 6 of them (17,7 %) being hybrids. Only 2 of the plants, however, had been cross-pollinated, but about half of their progeny (46,9 %) were hybrids.

The values of the spontaneous crossing obtained by using the above mentioned experimental method may scarcely be considered as the maximal ones, but they may yet be very near those. In order to obtain such maximal values it had surely been more convenient to leave only one plant of the variety to be tested. Cross-pollination between plants of the same isolation had then been avoided. In this case it should be necessary to sow several seeds in each isolation; immediately before the flowering a thinning out should take place so that only one single plant was left. I had no time to make such a thinning out, however, on account of other theoretical and practical investigations that were under way.

Another procedure is to sow one single seed of the variety to be tested in isolations located in sufficient large distances from each other (not in the cultures of beans) and to sow around it seeds from the other variety. The advantage of this method lies in the fact that it then is possible to compare the tendency of cross-pollination of two varieties with greater certainty than if the isolations are sown in the large bean-cultures, where generally many varieties are cultivated, and consequently the risk is at hand that the insown stock could be crossed with other plants than the surrounding. This method may be altered in such a manner that only one plant of each variety is allowed to remain in each isolation. In this case, however, the risk is close at hand that the visits of insects would be too few, resulting in a wrong interpretation of the data obtained.

The percentage of spontaneous crossings are in some cases relatively considerable; it would, therefore, be best to isolate the plants to be used for theoretical investigations. Special caution should be exercised in the judging of segregations which do not seem to be in correspondence whith the Mendelian ratios if the plants have not been isolated. A still more rigid criticism is required when supposed mutations are found. It becomes necessary to investigate whether these are

or are not the results of complicated segregations combined with coupling, in conformity with HERIBERT-NILSSON's (1916) theory.

With regard to practical breeding, it should be said, that spontaneous crossings as a rule have only a small disturbing effect, and no change should be made in the usual methods employed in the case of autogamous plants.

The fact of spontaneous crossing, no doubt, may be of certain importance for the seed-cultivation of the beans. If the seeds are not well sorted before the sowing a variety will soon degenerate owing to crossings with other varieties cultivated side by side, as often is the case. Indeed, it is a question whether or not such a variety as the chocolate brown bean, which in two years has given more than 4 % of bastards, should be cultivated close to other varieties.

Since the above was written (Oct. 1920) investigations on the same subject have been published by LENZ (1921 a and b) and SCHIEMANN (1921). Their investigations have not been made on material sown for this special purpose. The percentage of crossings, however, is about the same as in my trials.

My assumption stated in the beginning of this paper that nobody has made attempts to ascertain the percentage of crossing by way of experiments is wrong. SCHIEMANN states in her paper that MAYER-GMELIN and EMERSON have made such trials. Their results seem to be about the same as mine.

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FORTGESETZTE UNTERSUCHUNGEN ÜBER FATUOIDMUTATIONEN BEIM HAFER

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IN einer früheren Abhandlung (1911) habe ich die Entstehung und Vererbungsweise der eigenartigen *Avena fatua*-ähnlichen Mutationen bei reinen Linien von Hafer behandelt. Seitdem später die auffallend parallelen Speltoidmutationen beim Weizen konstatiert und näher untersucht worden sind, scheint es mir zweckmässig, die betreffenden Hafermutationen mit dem Namen Fatuoid-mutationen zu bezeichnen. Wie ich in meiner Abhandlung 1911 teilweise erörtert habe, sind nämlich diese Fatuoiden (in meiner Abhandlung 1911 »Atavisten» genannt) mit *Avena fatua* keineswegs identisch, besitzen aber gewisse Merkmale, die mit denjenigen von *A. fatua* übereinstimmen. Diese fatua-Merkmale beziehen sich auf Begrannung der Hüllspelzen, Behaarung des Callus und der Rachis und Ringwulst d. h. Ablösungsring der Blüten, wodurch die Ährchen frühzeitig abfallen bezw. zerfallen. Daneben bestehen auch mehrere Unterschiede von *A. fatua*: die Fatuoid-mutationen sind nicht wie meistens *A. fatua* an den Hüllspelzen behaart; Körnergrösse und Körnerform, Rispenbau usw. verhalten sich wie bei der entsprechenden Kulturhafersorte, und auch die Keimungsverhältnisse der Körner weichen von dieser nicht ab. Es ist somit ein bestimmter Merkmalkomplex von *A. fatua,* nicht aber der ganze, der bei den Fatuoidmutationen zum Vorschein kommt. Bei den Speltoidmutationen des Weizens ist, wie ich früher (1917) hervorgehoben habe, die Lage eine ganz entsprechende.

Der Fatuoid-komplex entsteht auf einmal durch Mutation und gibt in Verbindung mit dem Normaltypus die einfache mendelsche Spaltung. Zuerst entsteht aus dem Normaltypus ein Fatuoid-heterozygot, der in seiner Nachkommenschaft in einfacher Weise 1) Normalpflanzen 2) neue Heterozygoten 3) Fatuoiden ausspaltet. Der Fatuoidkomplex verhält sich demnach bei der Spaltung wie eine einfache Erbeinheit. Die drei Typen sind in mehreren von den gewöhnlichen Lehrbüchern und Handbüchern der Vererbungslehre erwähnt, bezw.

abgebildet (siehe z. B. Baur, Einführung in die experimentelle Vererbungslehre, 3—4 Aufl. 1919, S. 124, Plate, Vererbungslehre 1913, S. 159, Johannsen, Arvelighed 1917, S. 163, v. Hofsten, Ärftlighetslära 1919, S. 375), und ich kann deshalb in bezug auf die charakteristischen Unterschiede der drei Typen nur kurz auf diese allgemein zugänglichen Abbildungen hinweisen.

Auch bei den von Surface (1916) ausgeführten Kreuzungen zwischen *Avena sativa* und *A. fatua* gehen bei der sonst sehr komplizierten Aufspaltung die bezüglichen drei Merkmale, d. h. Begrannung, Behaarung am Callus bezw. an der Rachis und Ablösungsring, zusammen und verhalten sich wie eine Einheit. Sehr bemerkenswert ist aber der Befund von Surface, dass dies nicht ganz ausnahmlos der Fall ist, indem bisweilen der Komplex sich aufzulösen scheint. Nähere Data über solche Fälle sind vorläufig nicht publiziert worden. Nach dem von Surface mitgeteilten ist es jedoch schon sehr fraglich, ob der genannte Merkmalkomplex eine Abweichung in *einer* Erbeinheit darstellt oder ob nicht eher ein Komplex fest gekoppelter Erbeinheiten vorliegt.

Für die Speltoidmutationen glaube ich dies nachgewiesen zu haben (1920), und die Wahrscheinlichkeit wird dadurch noch grösser, dass auch die ganz analogen Fatuoidmutationen einen Erbeinheitskomplex umfassen, worauf ich schon (1920, S. 287) kurz hingewiesen habe. Die Untersuchungen von Surface und mir führen somit von verschiedenen Ausgangspunkten aus zu derselben präliminären Annahme.

Unter der Voraussetzung, dass die als eine Einheit vererbten fatuoiden Merkmale in Wirklichkeit einen gekoppelten Erbeinheitskomplex darstellen, sind die Fatuoidmutationen beim Hafer ebensowie die Speltoidmutationen beim Weizen als Komplexmutationen aufzufassen.

Wenn nun wirklich ein Komplex gekoppelter Erbeinheiten bei der Fatuoidenspaltung vorliegt, muss allerdings die Koppelung eine sehr starke oder eventuell absolute sein; denn vorläufig ist es mir hier nicht, wie bei den Speltoidmutationen, gelungen, eine Auflösung des Komplexes in der Nachkommenschaft von Fatuoidheterozygoten zu konstatieren, obwohl jetzt ein ziemlich grosses gesamtes Aufspaltungsmaterial im Laufe der Jahre untersucht worden ist.

Bisher haben nämlich in der Nachkommenschaft von Heterozygoten ausschliesslich die drei in meiner Abhandlung 1911 näher beschriebenen Typen ausgespaltet, d. h. Normalpflanzen, Heterozygoten und Fatuoiden. Intermediäre Bildungen sind zwischen diesen Typen

TABELLE 1.

Spaltungszahlen in der Nachkommenschaft von Fatuoidheterozygoten.

Reine Linie (über die Abstammung etc. der Linien vgl. meine Abhandlung 1911)	Jahr und Nummer	Anzahl von Pflanzen		
		Normaltypus	Heterozygot	Fatuoid
0197	1912—699	22	28	13
0201	1919—495	4	13	4
»	» —496	10	22	9
»	» —497	10	24	16
»	» —498	11	24	7
»	1920—637	36	54	18
Summe	—	71	137	54
0310	1912—701	6	9	1
»	1919—494	6	16	4
»	1920—636	16	24	4
Summe	—	28	49	9
01059	1912—702	22	28	21
»	1917—635	18	27	13
»	» —637	14	28	8
»	» —638	22	26	14
»	» —639	10	12	4
»	1919—501	19	25	10
»	» —502	15	24	10
»	1920—639	49	58	22
Summe	—	169	228	102
01060	1912—703	16	50	16
»	1917—643	6	12	6
»	» —645	11	16	7
»	» —646	15	38	13
»	» —648	13	29	20
»	1919—504	47	90	46
»	» —505	20	30	12
»	1920—640	17	35	14
»	» —641	15	26	6
Summe	—	160	326	140
01061	1912—704	29	45	36
»	1917—649	13	31	16
»	» —651	8	8	4
»	» —652	15	25	7
»	1919—506	17	41	11
»	1920—642	20	56	20
Summe	—	102	206	94

nicht aufgetreten, obwohl nach solchen absichtlich gesucht worden ist. Unter den Heterozygoten wurden von Herrn Dr. T. GANTE, der das Material des Jahres 1919 durchmusterte, Pflanzen gefunden, die in einzelnen Ährchen Begrannung sowohl auf der ersten als auf der zweiten Blüte aufwiesen und somit einigermassen in die Richtung von Intermediärbildungen zwischen Heterozygoten und Fatuoiden gingen. Wie die nachfolgende Mitteilung in diesem Heft von Dr. GANTE (1921) zeigt, sind aber diese Abweichungen nicht von erblicher Art, sondern modifikativ. Bei gewöhnlichen Heterozygoten kann m. a. W. hie und da Begrannung auch auf den oberen Blüten auftreten; die Dominanz des Normaltypus mit Hinsicht auf die Beschränkung der Begrannung auf die unterste Blüte ist nicht ganz vollständig, was auch an sich wenig Sonderbares bietet.

Vorläufig konnte also keine Auflösung des vermuteten gekoppelten Erbeinheitskomplexes bei dem vorliegenden Versuchsmateriale konstatiert werden. Die eventuelle Koppelung muss deshalb bei den Fatuoidheterozygoten ganz fest sein. Es ist jedoch beabsichtigt, bei einer von den Linien Heterozygoten in noch viel grösserem Massstabe anzubauen. Vielleicht wird doch schliesslich der Merkmalkomplex sich auflösen, so dass z. B. die fatuoide Begrannung ohne Vorhandensein des Ablösungsringes auftreten könnte oder umgekehrt, ebensowie beim Weizen Begrannung und speltoide Merkmale (an den Deckspelzen) sich von einander trennen können. Mehr als eine Annahme, die eine gewisse Wahrscheinlichkeit an sich trägt, ist dies jedoch vorläufig nicht.

In bezug auf die Spaltungszahlen haben die seit 1911 fortgesetzten Untersuchungen (vgl. die Tabelle) die einfache mendelsche Spaltung zwar durchaus bestätigt; es ist jedoch jetzt ziemlich offenbar, dass die Spaltung meistens nicht nach dem typischen Verhältnis 1 : 2 : 1 verläuft. Die Zahlen des Jahres 1919 sind als etwas unsicher zu bezeichnen, weil ein Teil der Pflanzen vor der Durchmusterung von Mäusefrass zerstört wurde. Es liegt jedoch kein Grund vor anzunehmen, dass dadurch das relative Verhältnis zwischen den drei Gruppen in nennenswerter Weise verschoben wurde. Bisweilen scheint die einfache Spaltung 1 : 2 : 1 vorhanden zu sein; im allgemeinen besteht aber eine mehr oder weniger deutliche Tendenz zur Verringerung der Zahl von Fatuoiden, was besonders bei der Linie 0310 hervortritt. Da es sich bei dem jetzt vorliegenden Versuchsmateriale immer deutlicher bestätigt hat (vgl. meine Abhandlung 1911, S. 19), dass die fatuoiden Pflanzen schwächlicher sind als die Normalpflanzen und Hetero-

zygoten, wird die zu geringe Zahl von Fatuoiden bei der Spaltung leichter verständlich, weil die schwächeren Pflanzen zweifellos mehr unter ungünstigen äusseren Umständen leiden. Ob die Schwächung sich auch auf die Gameten erstreckt, wie es beim speltoiden Weizen der Fall ist, ist noch nicht erwiesen worden. Ganz unwahrscheinlich ist dies nicht; denn bei einigen Linien (0197, 0310, 01059) scheinen die Normalpflanzen im Vergleich mit den Heterozygoten zu zahlreich zu werden, was bei den Speltoidheterozygoten des Weizens dadurch zustandekommt, dass der normale Pollen vor dem speltoiden Pollen bei der Befruchtung bevorzugt wird (vgl. meine Abhandlung 1921, S. 27—32). Es ist aber beim Hafer ein noch viel grösseres Versuchsmaterial nötig, um diese Frage beantworten zu können. Als Hauptresultat dieser Untersuchung ist also zu bezeichnen, dass die Spaltung stets ganz einfach geblieben ist, d. h. nur die drei erwähnten Typen hervorbringt.

In bezug auf die Mutationsfrage geben die fortgesetzten Untersuchungen nicht den geringsten Anlass zur Änderung in der von mir (1911) ausgesprochenen Auffassung, dass die hier vorliegenden fatuoiden Abweichungen wirkliche spontane Mutationen mendelnder Art darstellen. Dass die Heterozygoten aus spontanen Kreuzungen zwischen den betreffenden reinen Linien des Kulturhafers und *Avena fatua* entstehen sollten, ist aus den von mir (1911, S. 22—23) schon angeführten Gründen vollkommen ausgeschlossen. Wie ich in meiner Abhandlung in ausführlicher Weise erörtert habe, bleiben die sonstigen Eigenschaften der betreffenden reinen Linie (Rispentypus, Spelzenfarbe, Korngrösse, Kornform) bei der Mutation unverändert. Eine gelbspelzige Linie bleibt gelb, eine weissspelzige bleibt weiss, ein Fahnenhafer bleibt ein Fahnenhafer usw. Um Kreuzungen mit *A. fatua* als Ursache für das Entstehen der Fatuoidheterozygoten vorauszusetzen, würde man zu der nicht weniger als unsinnig zu bezeichnenden Annahme genötigt werden, dass z. B. weisse Haferlinien immer mit weissem Flughafer gekreuzt würden, gelbe Haferlinien immer mit gelbem Flughafer, Fahnenhafer immer mit Fahnenflughafer usw. Schon aus diesem einfachen naheliegenden Grunde sind die von ZADE (1912, 1918) diesbezüglich erhobenen Einwendungen als ganz hinfällig zurückzuweisen.

Eine einfache Spaltung nach Kreuzung mit *A. fatua* wäre überhaupt vollkommen unverständlich und würde den bei dieser, von v. TSCHERMAK (1914 a, 1914 b) und SURFACE (1916) experimentell ausgeführten und bearbeiteten Kreuzung gefundenen Tatsachen direkt

widersprechen. Im Gegenteil ist bei dieser Kreuzung, besonders nach SURFACE (1916), die Spaltung kompliziert. Die Farbenmerkmale spalten nämlich weitgehend unabhängig, sowohl unter sich, wie auch von dem Fatuoidkomplex und von der Spelzenbehaarung, so dass in F_2 viele verschiedene Kombinationstypen entstehen. Auch wird die bei anderen Haferkreuzungen häufige abgestufte Aufspaltung von der schwarzen Spelzenfarbe und der Begrannungsstärke an der unteren Blüte erwähnt. Die komplizierte Kreuzungsspaltung steht wie gewöhnlich zu der einfachen Mutationsspaltung im möglichst grössten Gegensatz.

Infolge der stets einfachen Spaltung ist es gleichfalls ausgeschlossen, wie ich schon früher (1911, S. 93) hervorgehoben habe, dass spontane Kreuzungen zwischen verschiedenen Kulturhafersorten die Ursache des Entstehens der Fatuoidheterozygoten sein können.

Die Ursache des Entstehens der Fatuoidheterozygoten kann somit jedenfalls unter keinen Umständen *ausserhalb* der reinen Haferlinien gesucht werden, sondern muss in der schon gegebenen Beschaffenheit der die Fatuoiden liefernden reinen Linie selbst liegen. Das dürfte wohl auch nunmehr die Meinung ZADES sein (1918, S. 223—224), die jedoch so unbestimmt und allgemein formuliert ist, dass sie der Kritik nicht leicht zugänglich ist. Wie ZADE sich die Bildung von Fatuoidheterozygoten aus zuerst konstanten Haferlinien vorstellt, ist ganz unklar. Es sind ja nicht die Haferlinien selbst, die Fatuoidheterozygoten sind. Mit Ausnahme von zwei sind sämtliche hierher gehörigen reinen Linien von Hafer von alten Landessorten durch Formentrennung gewonnen und sind vollkommen typische Kulturhaferlinien. Erst bei Vermehrung ergeben sie ganz vereinzelte Fatuoidheterozygoten. Es fehlt vollkommen jeder Anhaltspunkt dafür, dass die Haferlinien selbst in Fatuoidmerkmalen heterozygot sein sollten. Im Gegenteil spaltet ja in der Nachkommenschaft der Fatuoidheterozygoten die alte reine Linie als konstanter Homozygot vollkommen rein und typisch aus. Auf die ganz allgemeinen Äusserungen von ZADE, die, ohne die von mir mitgeteilten Tatsachen genügend zu berücksichtigen, den Ursprung meiner Fatuoiden in nicht näher bestimmter Weise in Kreuzungen mit *Avena fatua* suchen, kann ich deshalb nicht weiter eingehen.

Ein ernster Versuch, die Entstehung dieser und anderer rezessiver Mutationen durch Aufspaltung eines verdeckten Heterozygoten, (scheinbaren Homozygoten), also nicht durch wirkliche Mutation zu erklären, ist von HERIBERT-NILSSON (1916) gemacht worden. HERIBERT-NILSSON hat klar eingesehen, dass wenn die mutierende reine Linie

ein Heterozygot sein soll, so muss vor allem eine Erklärung ihrer weitgehenden Konstanz gegeben werden. Die Linie kann mit Hinsicht auf die mutierende Eigenschaft nicht monohybrid (monomer) sein; denn dann wäre die Entstehung eines von der Linie abweichenden und erst in seiner Nachkommenschaft Fatuoiden abspaltenden Fatuoidheterozygoten überhaupt unmöglich. Die reine Linie müsste nämlich direkt Fatuoiden ausspalten, was ja niemals der Fall ist. Der Unterschied zwischen Normaltypus und Fatuoid muss deshalb in zwei oder mehreren polymeren Erbeinheiten bestehen, aber auch das genügt nicht, denn man sollte dann auch Spaltungszahlen 15 : 1 oder 63 : 1 usw. erhalten, welche auch niemals bei sicheren Mutationen zu finden sind. Man muss deshalb die Hypothese von Koppelung heranziehen, und in dieser Weise baut HERIBERT-NILSSON eine geistvolle Theorie auf, die, auch wenn sie die erwünschte Erklärung in diesem und in anderen Fällen nicht geben kann, mir jedenfalls von grossem Interesse zu sein scheint und nicht unberücksichtigt bleiben kann.

Nach HERIBERT-NILSSON ist der »mutierende» Heterozygot im einfachsten Falle aus der Verbindung $\widehat{Ab} \times \widehat{aB}$ entstanden. Die Faktoren *A* und *B* sind homomer, verursachen jede für sich den Normaltypus; nur wenn beide fehlen (*ab*) entsteht der rezessive »Mutant». Infolge sehr fester Koppelung zwischen *A* und *b*, bezw. zwischen *a* und *B* werden nur sehr selten die Gametenkombinationen *AB* und *ab* gebildet. Die Verbindungen $Ab \times ab$ und $aB \times ab$ bilden die (bei sehr fester Koppelung) nur selten auftretenden Mutationsheterozygoten, die dann in ihrer Nachkommenschaft in einfacher mendelscher Weise den Normaltypus *AAbb* (bezw. *aaBB*), Heterozygoten *Aabb* (bzw. *aaBb*) und »Mutanten» (*aabb*) ausspalten. Die Theorie erfordert, dass der »mutierende» Heterozygot $\widehat{Ab} \times \widehat{aB}$ in seinem äusseren Aussehen von den wirklich homozygoten Verbindungen $Ab \times Ab$ und $aB \times aB$ nicht zu unterscheiden ist. Zusammen ergeben diese drei Genotypen einen scheinbar homozygoten Typus, eine scheinbar reine Linie, deren Konstanz bei sehr fester Koppelung nur selten durch die Neukombinationen (»Mutationsheterozygoten») $Ab \times ab$ und $aB \times ab$ gestört wird. Dass der »Mutationshomozygot» $ab \times ab$ in der Nachkommenschaft des Heterozygoten $\widehat{Ab} \times \widehat{aB}$ überhaupt nicht gefunden wird, scheint nicht sonderbar; denn je fester die Koppelung, desto seltener muss der »Mutationshomozygot» im Vergleich mit den »Mutationsheterozygoten» auftreten.

So weit ist die Theorie ganz klar, die Schwierigkeit derselben liegt

aber vor Allem darin, dass der Heterozygot $\widehat{Ab} \times \widehat{aB}$ in seiner Nachkommenschaft regelmässig zur Hälfte wirkliche Homozygoten $Ab \times Ab$ und $aB \times aB$ ergeben muss, *welche nach der Theorie nicht weiter »mutieren» können.* Wenn man also in der Nachkommenschaft eine Pflanze zur Weiterzucht herausnimmt, ist die Chance 1 gegen 1, dass man einen Homozygoten bekommt, der dann nicht weiter mutieren kann. Nun waren aber fast sämtliche hier in Frage kommenden mutierenden Haferlinien solch einer mehrmaligen (2—6-jährigen) Pedigreeauslese unterworfen, bevor sie die in meinen Abhandlungen beschriebenen Fatuoidmutationen ergaben. Es ist deshalb ganz unwahrscheinlich, dass die Auslese nicht zur Homozygotie geführt habe, was ja bei der Auslese mit der Chance 1 gegen 1 rasch erfolgen müsste. Aus demselben Grund ist die Theorie von HERIBERT-NILSSON auch nicht auf die anderen von mir beschriebenen Getreidemutationen (Spelzenfarbemutationen beim Hafer, Chlorophyllmutationen bei Gerste, Speltoidmutationen beim Weizen) anwendbar, womit nicht gesagt werden soll, dass sie nicht für andere Mutationen gültig sein mag.

Damit fällt auch die Annahme von v. TSCHERMAK (1914 a, S. 309), dass die Kulturhaferlinien teilweise konstant, teilweise weiterhin ausspaltend sein sollten.

Die Annahme von Mutation bei den in dem betreffenden Merkmal homozygoten Linien muss deshalb für meine Fatuoiden aufrecht erhalten werden. Wie ich in meiner Abhandlung 1911 schon hervorgehoben habe, wird damit selbstverständlich nicht verneint, dass auch durch natürliche Kreuzungen mit *Avena fatua* fatuoidähnliche Bildungen entstehen können. Es sind ja manche Fälle bekannt, wo etwa dieselben Typen durch Kreuzung und durch Mutation entstehen können. Die von mir in Schweden gefundenen, aus Fatuoidheterozygoten ausgespaltenen Fatuoiden gehören indessen ausnahmslos zu den Mutationen.

Selbstverständlich wird damit nichts über die Ursache oder das wirkliche Zustandekommen der Mutation gesagt. Ich wenigstens lege in den Begriff der Mutation weiter nichts hinein, als dass dadurch eine spontane erbliche Abänderung zustandekommt, die mit Kreuzung und Kreuzungsspaltung, nach allen bis jetzt bekannten Tatsachen zu schliessen, nichts zu tun hat. In welcher Weise, d. h. durch welche Veränderung der Erbsubstanz, die Mutation entsteht, ist ja noch immer eine ganz offene Frage. Wenn dabei von Wegfallen oder Verlust eines Erbfaktors gesprochen wird, so wird jeder Vererbungsforscher darunter nichts anderes verstehen als eine rein

äussere Ausdrucksweise, die den Unterschied zwischen den beiden Gliedern eines Allelomorphenpaares hervorheben und die Veränderung von *A* zu *a* bezeichnen will, die aber über den wirklichen inneren Vorgang der Abänderung natürlich nichts aussagt.

Wenn man dagegen nur in ganz allgemeiner Weise Mutationen wie die hier beschriebenen als Folgen von Kreuzungen stempeln will, ohne auf das dagegen sprechende Tatsachenmaterial einzugehen, so ist dies eine unzulässige Vereinfachung der Sachlage, die nur das Problem verdeckt und von einem näheren Verständnis desselben entfernt.

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ÜBER EINE BESONDERHEIT DER BEGRANNUNG BEI FATUOID-HETEROZYGOTEN

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DIE zuerst von NILSSON-EHLE beschriebene Wildhafermutation des Kulturhafers zeichnet sich bekanntlich dadurch aus, dass die Ährchen an allen Deckspelzen begrannt sind, und dass an der Ährchenachse (Rachis) starke Behaarung und an der Basis der einzelnen von Spelzen umgebenen Körner ebensolche Behaarung und ein charakteristischer Ringwulst auftritt, der bewirkt, dass bei der Reife des Kornes dieses ausserordentlich leicht aus dem Blütenstande herausfällt. Das normale *Avena sativa*-Ährchen besitzt dagegen, je nach der Sorte, nur eine oder keine Granne an der Spelze des untersten Kornes, schwache oder keine Behaarung an dessen Basis und der Rachis und keinen Ringwulst.

Diese Mutation wurde von NILSSON-EHLE als eine Verlustmutation mit Wegfall eines Hemmungsfaktors gedeutet, und die oben beschriebene Form würde die homozygote Mutante darstellen. NILSSON-EHLE fand nun eine heterozygote Mutante, die bei Aussaat nach dem einfachen Mendel'schen Schema in etwa 25 % Normale, 50 % heterozygote und 25 % homozygote Mutanten aufspaltet. Der Heterozygot ist etwas kräftiger begrannt als die Normale, aber nur am untersten Korn — die Granne stärker gekniet —, etwas stärker behaart an der Basis des untersten Kornes, oft auch an der Rachis, besitzt jedoch keinen Ringwulst.

Beim Auszählen derartiger Nachkommenschaften fielen mir unter den Heterozygoten Pflanzen mit Ährchen auf, bei denen entweder alle Körner begrannte Spelzen oder bei einer Sorte mit häufig auftretenden dreikörnigen Ährchen (0201) zwei Körner des Ährchens — und zwar die untersten — begrannte Spelzen besassen. Ein Ringwulst, wie bei den homozygoten Mutanten schien nicht vorhanden zu sein. Die Basis- und Rachisbehaarung war jedoch in einzelnen Fällen bei den Zwei-Grannenährchen stärker als bei den übrigen Ährchen derselben Pflanze [1]. (Heteroz. aus Sorte 01059).

[1] Das Material wurde mir von Herrn Prof. NILSSON-EHLE freundlichst zur Bearbeitung überlassen.

Diese Beobachtungen wurden gemacht bei Heterozygoten der Sorten:

0201 (normal) von NILSSON-EHLE (1911) wie folgt charakterisiert: Schwarzkörnige, ziemlich stark begrannte *Fahnenhafersorte* aus schwarzem Tartar. Fahnenhafer. Begrannungsfrequenz 32 %. Granne nicht gekniet, Basis- und Rachisbehaarung schwach.

01059 (normal) schwarzkörnige, ziemlich stark begrannte *Rispensorte* aus schwarzem, Schwed. Rispenhafer. Begrannungsfrequenz 94 %. Grannen bisweilen, d. h. an gewissen Ährchen mit ziemlich langem unteren schwarzen Teil und dann auch etwas gekniet. Basis- und Rachisbehaarung schwach.

Beide Sorten gingen in NILSSON-EHLE's frühere Versuche (1911) ein.

0450 (normal) »Grossmogul», eine Sorte die ich folgendermassen beschreiben möchte: [1]

Schwarzkörnige, stark begrannte *Rispenhafersorte*, Begrannungsfrequenz 100 %, Grannen mit ziemlich langem, schwarzen gedrehten Teil, vielfach schwach gekniet, Basis- und Rachisbehaarung schwach; neben an der Basis unbehaarten untersten Körnern kommen solche mit einzelnen langen Basishaaren vor.

Was nun die Zweigrannigkeit angeht, so war man geneigt an die Bildung einer Zwischenform oder evtl. an eine Fatuoidknospenmutation zu denken. Gegen letztere sprach freilich die mangelnde Ausbildung des Ringwulstes und die Tatsache, dass bei der Form mit dreikörnigen Ährchen nur zwei Körner begrannte Spelzen besassen.

Um genaueren Aufschluss zu bekommen wurde das Material im Jahre 1920 ausgesät, und zwar getrennt, die Körner der eingrannigen und mehrgrannigen Ährchen von je einer Pflanze. Das Ergebnis war das folgende (Tab. 1 und 2).

Es erweist sich also, dass die zweigrannigen Ährchen keine Knospenmutationen sind, sondern dass sie, wie die eingrannigen Ährchen in Normale, heterozygote Mutanten und homoz. Mutanten aufspalten. Dass die Zahlen so wenig mit der Mendel'schen Proportion übereinstimmen, liegt wohl an der schlechten Keimung: 374 Körner lieferten nur 178 Pflanzen! Ausserdem stand mit N:o 3002 keine ganze Pflanze, sondern nur eine lose Rispe zur Verfügung.

Beim Durchsehen des Materials ergab sich, dass unter den Heterozygoten in 5 Nummern wiederum Pflanzen mit sowohl eingrannigen wie zweigrannigen Ährchen vorkamen. Die charakteristische Ring-

[1] Die Beschreibung stützt sich auf Material von Normalen aus der unten zu beschreibenden Spaltung.

TABELLE 1.
Zweigrannige Ährchen.

N:o Jahr 1920	Sorte	ausgesät	geerntet	Resultat
3001 A	0201	1 Ährchen = 3 Körner	3 Pfl.	1 Normal 1 heteroz. M. 1 homoz. M.
3002 A	01059	1 Ährchen = 2 Körner	2 Pfl.	1 heteroz. M. 1 homoz. M.
3003 A	0450	5 Ährchen = 10 Körner	8 Pfl.	3 Normale 4 heteroz. M. 1 homoz. M.
				norm. : heteroz. : homoz. 4 : 6 : 3

TABELLE 2.
Eingrannige Ährchen.

N:o Jahr 1920	Sorte	ausgesät	geerntet	Resultat
3001 B	0201	107 Körner	28 Pfl.	2 Normale 15 heteroz. M. 11 homoz. M.
3002 B	01059	34 Körner (1 Rispe)	26 Pfl.	8 Normale 17 heteroz. M. 1 homoz. M.
3003 B	0450	218 Körner	111 Pfl.	48 Normale 54 heteroz. M. 9 homoz. M.
				norm. : heteroz. : homoz 58 : 86 : 21.

Gesamtspaltung: 62 : 92 : 24.

wulstbildung wurde in keinem Falle bei den zweigrannigen Ährchen festgestellt.

Es liegt hier also augenscheinlich eine ausgeprägt starke Begrannungstendenz vor, die modifikativ in der Weise zur Geltung kommt, dass sie sich in Zweigrannigkeit bei manchen Ährchen äussert. Diese Begrannungstendenz ist bei der Nummer 3003 (Grossmogul) so stark, dass sogar, bei *normalen* Pflanzen zweigrannige Ährchen auftreten [1].

[1] Es waren dies durchaus typisch Normale. Eine Aussaat des betreffenden Materials will ich demnächst ausführen um etwaigen Einwänden zu begegnen.

Die Durchsicht wurde insofern nicht ganz genau vorgenommen, als im allgemeinen nur die zweiten Grannen berücksichtigt wurden, die eben aus der Spelze herausragten, also ohne weitere Manipulationen sichtbar waren. Es ist möglich, dass mir infolgedessen einige zweite Grannen entgangen sind. Das Resultat wird auch dadurch beeinflusst, dass immer eine Reihe von Körnern beim Transport herausfallen.

Die meisten Pflanzen mit Zweigrannenährchen wurden bei den Heterozygoten der N:o 3003 (0450) beobachtet, auch hatte diese Nummer die zahlreichsten zweigrannigen Ährchen auf ein und derselben Pflanze (oft 3 bis 4). Der Elter hatte sogar 6 zweigrannige Ährchen besessen, von denen 5 ausgesät wurden. (Vergl. Tab. 1).

TABELLE 3.

No.	Heteroz. Pfl. mit *Ein- u. Zwei-gr.* Ährchen	Heteroz. Pfl. mit *nur Ein-gr.* Ährchen
3001	3	13
3002	2	16
3003	40	18
No.	**Normale Pfl. mit *Ein- u. Zwei-gr.* Ährchen**	**Normale Pfl. mit *nur Ein-gr.* Ährchen**
3003	4	47

Bei den Nummern 3001 und 3002 bemerkte ich keine zweite Granne an den Ährchen von normalen Pflanzen. Allerdings ist die Zahl der Normalen sehr gering — 3 resp. 8. Bei diesen Nummern ist die Begrannungstendenz weniger stark, so dass neben begrannten vollständig grannenlose Ährchen vorkommen (vgl. Sortenbeschreibung). Dagegen tragen die Normalen der N:o 3003 nur begrannte Ährchen!

Im Folgenden möchte ich eine kurze Schilderung von meinen aufbewahrten Proben von Zweigrannen-Ährchen geben.

BESCHREIBUNG DER ZWEIGRANNENÄRCHEN.

N:o 3001 (0201) heteroz. 1) Die Granne des ersten Kornes gekniet und Basisbehaarung schwach, wie bei Eingrannenährchen der Heterozygoten im allgemeinen. Von Rachisbehaarung kann man sowohl bei Ein- wie Zweigrannenährchen kaum reden. Die Granne des zweiten

Kornes nicht gekniet, fadenförmig, bogenförmig gekrümmt. (Ich sammelte hier leider nicht Eingrannenährchen von der gleichen Pflanze.)

N:o 3002 (01059) heteroz. 2) Die Granne des ersten Kornes gekniet, wie bei den Eingrannenährchen derselben Pflanze. Basis- und Rachisbehaarung kräftig, ungefähr gleichstark wie bei den letzteren. Zweite Granne schwach gekniet.

3) Ein Ährchen von einer anderen Heteroz. verhält sich ebenso, doch ist hier die zweite Granne scharf gekniet.

N:o 3003 (0450) heteroz.

4) Die Granne des ersten Kornes gekniet wie bei Eingrannenährchen, Basis- und besonders Rachisbehaarung stark, *wirkt etwas kräftiger* als bei Eingrannenährchen derselben Pflanze. Die Granne des zweiten Kornes sehr schwach gekniet.

5) Zweite Granne deutlich, wenn auch schwach gekniet.

6) Zweite Granne schwach, fadenförmig, (ohne schwarzen gedrehten Teil, steil aufrecht.

N:o 3003, (0450) normal.

7) Erste Granne kaum gekniet, wie bei Eingrannenährchen von Normalen, zweite Granne fadenförmig; Basis- und Rachisbehaarung im Vergleich zu Eingrannenährchen derselben Pflanze nicht untersucht; im Vergleich zu Eingrannenährchen von normalen Pflanzen im allgemeinen, scheint sie gleichschwach wie bei diesen zu sein.

Um festzustellen, ob die Ausbildung der Zweigrannenährchen vielleicht von dem Sitze an der Spitze einer Rispe oder eines Hauptastes abhängig wäre, d. h. ob etwa eine Ernährungsmodifikation in diesem Sinne vorläge, untersuchte ich das Material daraufhin, vor allem die Nummer 3003. Der Sitz der Ährchen zeigt hiernach nur eine gewisse Regelmässigkeit.

Von 48 Ährchen, deren Sitz festgestellt wurde, sassen:

4 an der Spitze einer Rispe,

33 » » » von mehr oder minder kräftigen Rispenästen erster Ordnung (darunter 16 einährigen).

Um einige Beispiele anzuführen, so traten bei Heterozygoten der N:o 3003 (0450) die Zweigrannenährchen in folgender Weise auf:

I) Rispe 1. An der Spitze des zweitstärksten Astes der untersten Verzweigung.

Rispe 2. Drittes Ährchen von oben.

Rispe 3. Ein Spitzenährchen, Spitze der Rispe.

Ein Spitzenährchen des stärksten Astes der untersten Verzweigung.

II) Eine Rispe. An der Spitze des zweitstärksten Astes der zweituntersten Verzweigung.

III) Eine Rispe. Zweites Ährchen des stärksten Astes der dritten Verzweigung von oben.

ZUSAMMENFASSUNG.

Zusammenfassend lässt sich sagen:

1) Die hier beschriebene partielle Zweigrannigkeit beruht nicht auf Knospenmutation.
2) Dass keine Zwischenform vorliegt, darauf weist das Auftreten der Zweigrannenährchen bei Normalen der Sorte 0450 hin.
3) Es handelt sich wohl vielmehr um die Modifikation einer Sorteneigenschaft: Starker oder relativ starker Begrannung.

Eine Sorte (0450) mit starker Begrannung besitzt unter den Normalen in geringer Zahl Pflanzen mit Ein- und Zweigrannenährchen. In bedeutend grösserer Menge finden sich solche Pflanzen unter den Fatuoid-Heterozygoten dieser Sorte, wo ja die Begrannung verstärkt werden soll [1].

Einige Sorten (0201; 01509) mit etwas schwächerer Begrannungstendenz zeigen derartig modifizierte Pflanzen erst unter den Heterozygoten.

Inwieweit diese Modifikation in der Häufigkeit ihres Auftretens durch äussere Umstände (Boden- und Witterungsverhältnisse) beeinflusst wird, wäre noch zu untersuchen.

ZITIERTE LITERATUR.

1. Nilsson-Ehle, H. 1911. Ueber Fälle spontanen Wegfallens eines Hemmungsfaktors bei Hafer. — Zeitschr. f. Ind. Abst. u. Vererbungsl. 5. S. 1—37.
2. Zade, A. 1918. Der Hafer. — Eine Monographie auf wissenschaftlicher und praktischer Grundlage. Gust. Fischer, Jena.

[1] Zade (1918, S. 74), der, nebenbei bemerkt, an Nilsson-Ehles Fatuoid-mutationen nicht glauben will, sagt in seiner allgemeinen Beschreibung der Spelzfrucht von *Avena sativa* über die Granne: »In den seltenen Fällen, in denen man sie bei Körnern höherer Ordnung antrifft, handelt es sich bis auf verschwindende Ausnahmen um die schon erwähnten Kreuzungen aus Wild- und Kulturhafer.»

CORRIGENDA.

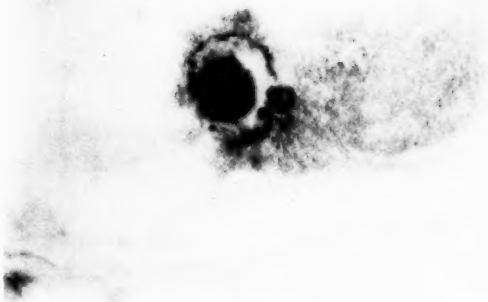
S. 165. Z. 10 v. u. steht XIV, lies XXV.
» 185. » 7 v. o. » *AA*, » *Aa*.
» 276, » 11, 10 und 5 v. u. steht *MM* bezw. *mm*, lies *RR* bezw. *rr*.

Page 342, line 23, for »*V*» read »*F*».
» 361, » 12, » »24» » »23».

1. Blue. 2. Violet. 3. Bluishred. 4. Pure red.

5. Tinged blue. 6. Tinged red. 7. Earth-brown, non-marbled. 8. Earth-brown, marbled.
9. Rust-brown, non-marbled. 10. Rust-brown, marbled. 11. White.

Cederquists Graf. A.-B., Sthlm



Da die Fig. 6, S. 96 dieses Jahrganges zu der Abhandlung von K. V. Ossian Dahlgren (Vererbungsversuche mit einer buntblättrigen Barbarea vulgaris) bei der Reproduktion misslungen ist, fügen wir hier eine neue Abbildung bei.

TILL MEDARBETARNA.

Manuskript — helst *maskinskrivna* — torde insändas till Redaktionen (Adelgatan 7, Lund) i fullt tryckfärdigt skick. De böra vara *noga genomsedda* för undvikande av ändringar mot manuskriptet. Obs. kommateringen! Korrektionskostnaderna betalas av författaren. Korrektur ställes till Redaktionen. Direkt förbindelse mellan författaren och tryckeriet tillåtes icke.

Personnamn sättas med KAPITÄLER. De markeras i manuskriptet med en våglinje. Latinska namn på växter och djur samt ord och satser av särskild vikt *kursiveras* (enkel understrykning).

Figurer numreras med arabiska siffror. Figurförklaring (på avhandlingens språk) torde insändas *samtidigt* med illustrationsmaterialet.

Planscher numreras med romerska siffror och de i dem ingående bilderna med arabiska.

Tabeller åsättas arabiska siffror och förses med kort rubrik.

Citerade arbeten samlas i en litteraturförteckning. I texten hänvisas till denna genom angivande av författare och årtal. Har en författare utgivit flera publikationer under samma år, tilläggas efter årtalet små bokstäver (a, b, c, etc.). Samma beteckningssätt användes i litteraturlistan, vilken uppställes i alfabetisk ordning efter författarna och under dessa i kronologisk följd. Inga litteraturhänvisningar få göras genom fotnoter. Över huvud så få noter som möjligt!

Avhandlingarna skola vara skrivna på tyska, engelska eller franska. Det är önskvärt, att uppsatser på tyska åtföljas av en resumé på engelska. Översättningar, som ombesörjas av Redaktionen, bekostas av författaren.

Åt varje författare lämnas 100 fria separat. Avhandlingar på ett ark och däröver förses gratis med särskilt omslag. Till ett pris av 10 kr. pr 100 st. lämnas, om så önskas, omslag till mindre uppsatser. Större antal särtryck fås till självkostnadspris.

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